THE BREEDING ECOLOGY OF FOUR SPECIES OF HERONS AT LAKE ALICE, ALACHUA COUNTY, FLORIDA

By

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PREFACE AND ACKNOWLEDGMENTS

In 1957, Florida was emerging from a severe drought. The long dry period, coupled with the continuing destruction of long-legged wading bird habitat which has accompanied the development of Florida, seemed to be bringing the numbers of long-legged wading birds to dangerously low levels.

Officials of the Florida Audubon Society were greatly concerned over this decline and as a result established a three year research grant to support a study of the basic ecology of herons. Their interest made this study possible and to this conservation organization I am deeply indebted. Mr. John H. Storer and Miss Lisa Von Borowsky, president and vice-president of the Florida Audubon Society generously shared with me the benefits of their many years of heron observations in Florida. The National Wildlife Federation was also concerned and in 1959 awarded the study a research grant, and to them I am also indebted. The Florida Academy of Sciences awarded the study a research grant in 1959.

Access to Lake Alice was arranged with the cooperation of the staff of the Agricultural Experiment Station. I appreciate the help of several fellow graduate students who assisted in identifying food items and accompanied me on trips.

Chairman of my supervisory committee, Dr. J. C. Dickinson, Jr., was of assistance throughout my work and I gratefully acknowledge his help. Other members of my committee gave willingly of their time and counsel and I especially appreciate their critical reading of this dissertation.

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INTRODUCTION

There is a large literature dealing with the herons and egrets. Most of this literature consists of: (1) examples of unusual feeding behavior in this highly adaptive group; (2) unusual geographic records of these birds, which wander extensively after the breeding season; (3) records of soft part colors, which appear to vary with the season in at least some species; (4) discussions of their all-white coloration; and (5) general observations on the location, size, and species composition of local and, sometimes, newly established heronries. In the last decade the literature has been swelled by reports on the remarkable range expansion of the Cattle Egret (Bubulcus ibis). But all this literature does little to clarify the total biology of these birds. Although we may never know as much about them as we know about the birds that nest in more readily available places, there have been some recent studies that aid greatly in our understanding of these birds.

Meyerriecks (1960) published a detailed discussion of the breeding behavior of the Green Heron (Butorides virescens) and made an interesting introduction to the comparative ethology of the Ardeidae by comparing the Green Heron with four other species. Valverde (1955) studied the large mixed heronry at Camargue, France, and has published the best account of ardeid ecology to date. There have been a few reports on the breeding behavior of various species. Noble and Schmidt (1938), Allen

and Mangels (1939), and Noble (1942) wrote about the Black-crowned Night Heron (Nycticorax nycticorax), and Verwey (1930) published on the Gray Heron (Ardea cinerea). Weller (1961) discussed certain aspects of the post-laying breeding biology of the Least Bittern (Ixobrychus exilis). There has been no systematic study of the ecology of a mixed breeding colony.

Purpose of the Study

The most common herons of the Gainesville, Florida area, are the Snowy Egret (Leucophoyx thula), Little Blue Heron (Florida caerulea), Louisiana Heron (Hydranassa tricolor), and Cattle Egret. At the start of my study these appeared to have basically identical ecology, except for the conspicuously different feeding habits of the Cattle Egret. My purpose was to gather information on the virtually unknown basic breeding biology of these four species, to study their feeding behavior, and finally to study the food habits. The aim was not only to learn the facts, but also to learn something about the birds' interspecific relationships, and their relationship to their environment, especially to the most interesting but least known part of their environment, the heronry. I hoped that such a study would provide information that could help explain what a heronry is, what it provides the birds, and would perhaps eventually help solve the intriguing problem of why even undisturbed ardeids will abandon one area long used as a heronry to breed in another as yet untried area. Though progress has been made, a full and deep understanding of the heronry is still distant. We need still to learn a great deal more about the lives of the individual birds as well as the individual species, and especially we need to learn the role of the heronry in their lives.

STUDY AREAS AND METHODS

Most of the observations reported here were made near Gainesville, Alachua County, Florida, primarily at Lake Alice and Payne's Prairie, but observations were made in many other areas. The climate of the area is nearly semi-tropical and the long summers are hot and wet with high relative humidity. The winters are short, mild, and considerably drier than the summers. The temperature usually goes below freezing several times during the winter months. Figure 1 shows the temperature-rainfall relationships based on averages of data obtained from 1954 through 1960 at the weather station adjacent to Lake Alice (Anonymous, 1961).

The Gainesville Area

Gainesville, just southeast of the center of Alachua County, Florida, is located in the Central Highlands near the northern end of the Florida Peninsula (Cooke, 1945) and is about midway between the Atlantic Ocean and the Gulf of Mexico (see Figure 2). The area around Gainesville supports a large number of herons. The terrain is mostly gently rolling hills with innumerable ponds and sinks and with several large wet prairies and lakes south of Gainesville. Pine flatwoods extend northeast of the city. The elevation varies from a maximum of about 200 feet to about 50 feet near which latter level lie the large wet prairies in the southern part of the county. The area is underlain by limestone and part of the uplands show karst topography. Practically all the soils are fine sand originally derived from Coastal Plain sediments (Taylor *et al.*, 1954).

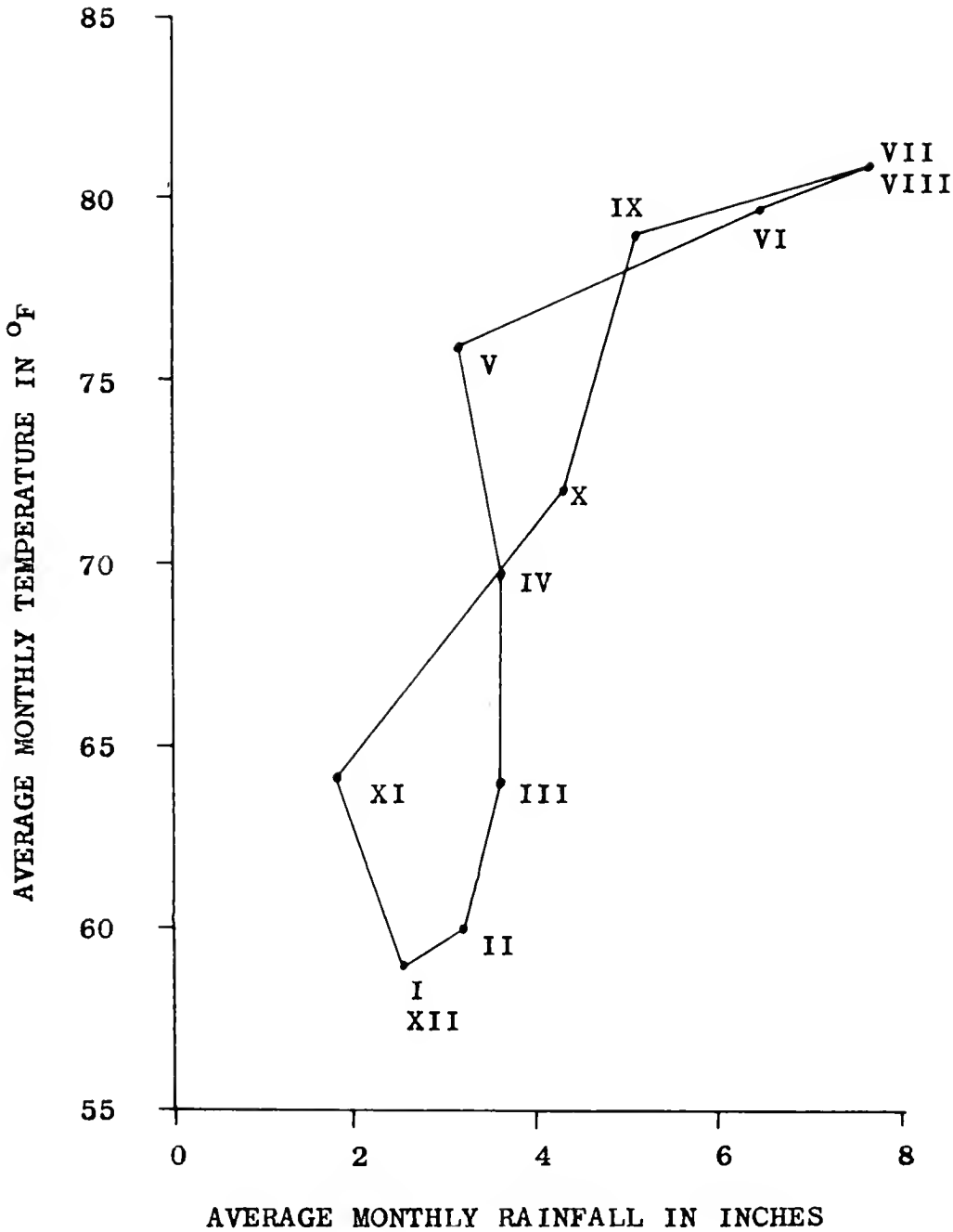

Figure 1: Temperature-rainfall relationships at Lake Alice, averages of data gathered 1954-1961 (Anonymous, 1961).

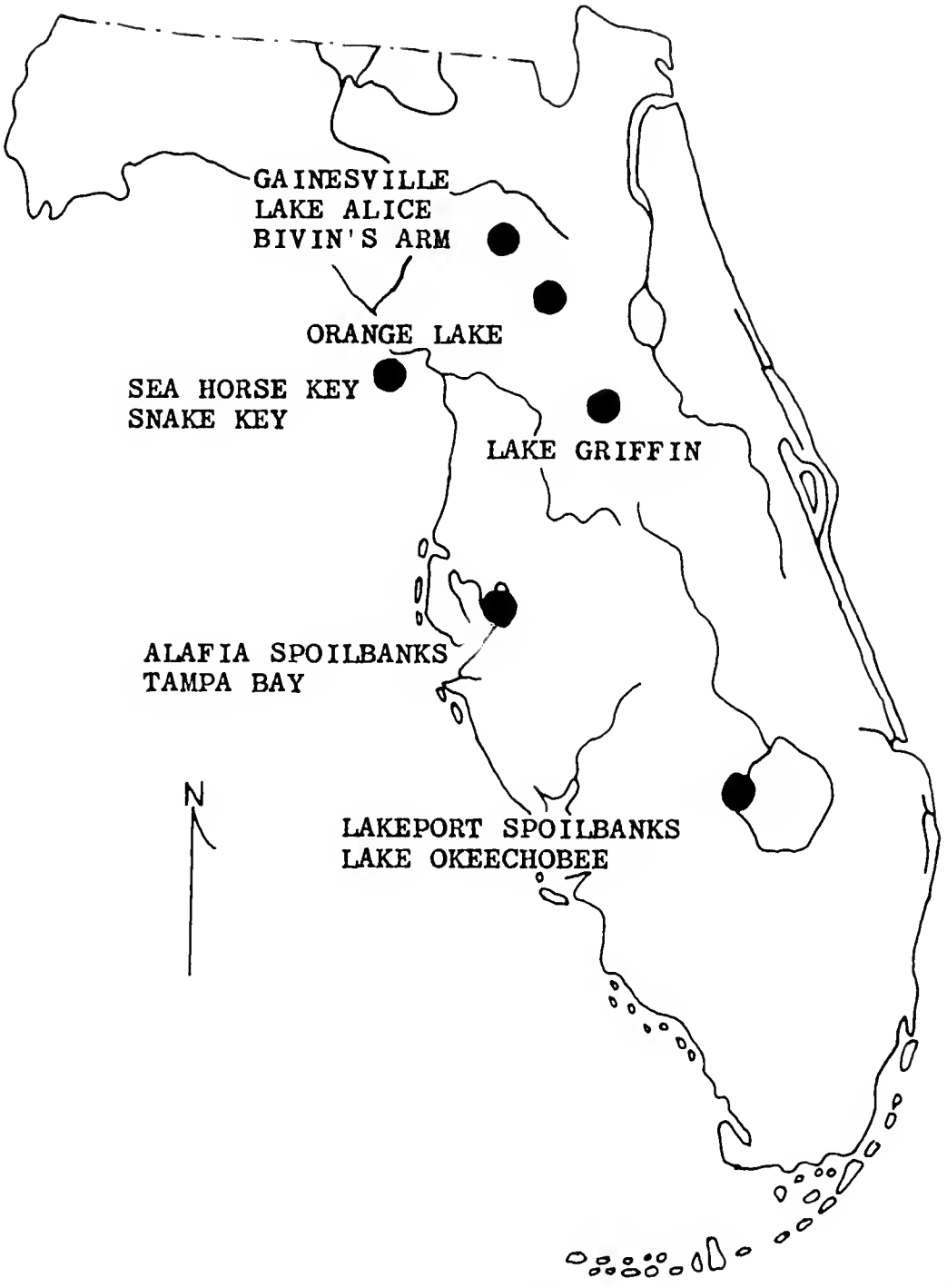

Figure 2: Map of peninsular Florida showing location of heronries and other major points mentioned in text.

There are three major types of vegetation: hardwood hammocks, pinelands, and wet lands. The more hydric hammocks around the prairies and lakes are characterized by magnolia (Magnolia grandiflora), water-oak (Quercus nigra), laurel-oak (Quercus laurifolia), and cabbage palm (Sabal palmetto), and the more open upland hammocks by live-oak (Quercus virginiana), hickory (Carya aquatica), and sometimes longleaf (Pinus australus) or loblolly pine (Pinus taeda). There is practically no mesic hammock in the area today; most of it has been cut over, and much of it has been cleared for agricultural or other development. Northeast of Gainesville there are extensive pine flatwoods dominated by slash pine (Pinus palustris) and saw-palmetto (Serenoa repens) with numerous bald-cypress (Taxodium distichum) and loblolly-bay (Gordonia lasianthus) ponds. There are also flatwoods scattered throughout the area and a few undulating areas of longleaf pine (Laessle, 1942, and Taylor et al., 1954).

The extensive wetlands are responsible for the large heron population in the Gainesville area; and the most important of these wetlands is Payne's Prairie or Alachua Lake, which in recent years has been the principal feeding area for herons around Gainesville. This nearly level prairie varies from permanently flooded to, especially around the edges, dry land. Much of it is covered with between one inch and two feet of water, but during the wet summer season the water rises and covers practically all the prairie. The vegetation of the deeper parts of the prairie include water-hyacinth (Eichhornia crassipes), pickerel weed (Pontederia lanceolata), arrowhead (Sagittaria spp.), and others, while the shallower and seldom flooded parts of the prairie support dog-fennel (Eupatorium spp.), maidencane (Panicum hemitomum), and a wide variety of other grasses.

There are other wet prairies in the area. Levy Lake, Ledwith Lake, Tuscawilla Lake, Kanapaha Prairie, and Hogtown Prairie are the larger and more important of these areas. They are all similar to Payne's Prairie and they are covered with similar vegetation. The differences between them are primarily due to different water depths. In addition to these prairies there are extensive marshes and wetlands surrounding Orange Lake, slightly farther south; and there are innumerable small prairies, ponds, sinks, and marshy shore lines with vegetation similar to the Payne's Prairie throughout the region. Practically all of these areas are used by the herons for feeding, at least occasionally.

Heronries near Gainesville

Social herons have nested in at least three separate colonies in the Gainesville area. A floating island, Bird Island, in Orange Lake has supported a heronry for many years (Baynard, 1912). A moderate sized group of herons bred in emergent trees and bushes in Bivin's Arm just south of Gainesville for many years (Dickinson, 1946). Since 1948 there has been a large mixed heronry at Lake Alice on the University of Florida campus. In 1948 the herons failed to breed at Bivin's Arm and have apparently never made any effort to re-establish themselves there. These appear to be the birds that occupied Lake Alice. The vegetation of these three areas is quite similar. The trees and bushes for the most part are the same species. Besides their vegetation these three heronries have other things in common. They are surrounded by water at least several feet deep, there are alligator populations, and there is practically no predation, and human disturbance is minimal. It is apparently these factors plus the presence of suitable nest sites and

nesting material that were of prime importance in the original establishment of these heronries. The less social Green Heron and Least Bittern nest at several other localities around Gainesville in addition to these three heronries.

Description of Lake Alice

Because most of the observations presented later in this report are based on data gathered at Lake Alice, I shall describe this heronry in more detail. Lake Alice was originally a small pond of about 10 acres, but it fluctuated considerably (Dickinson, 1940). As the University of Florida campus grew, surface runoff increased. In 1948 an earthen dam was built just west of the "lake." The hollow where lay Jonah's Sink, as it was formerly called, was flooded and the water spread out over an area of about 90 acres. Included in this newly flooded area were a low lying buttonbush (Cepalanthus occidentalis) marsh and the margins of an extensive hammock of live oak, loblolly pine, and sweet-gum (Liquidamber styraciflua), all of which were killed by the water. Buttonbush replaced the hammock trees and wax myrtle (Myrica cerifera), willow (Salix spp.), red maple (Acer rubrum), and elder (Sambucus simpsonii) invaded areas of shallow water. Water pennywort (Hydrocotyle spp.) grew over the top of the water throughout the swamp area, water-hyacinth grew over deeper but still sheltered water. Pickerel weed, broad-leafed cattail (Typha latifolia), smartweed (Polygonum spp.), and many other emergents invaded the periodically flooded lake margins. What attracted the herons to Lake Alice, at least what they used when they first arrived at the lake, were the bushes and trees in which they nested. The species of bush or tree did not appear to be of any importance; it appears that the only thing the trees or bushes must provide the herons is a physically

suitable nest site. To be acceptable to herons for nest sites, the trees must be located in a place difficult of access to predators. Thus Florida heronries are usually on islands or over deep water.

Besides nesting in red maple, buttonbush, elder, wax myrtle, and willow in Lake Alice, they nest elsewhere in Florida, in such diverse vegetation as mangroves, cabbage palms, black gum, bald-cypress, maiden-cane, and others. Thus it must be reasons other than the kinds of nest trees available that caused the herons to nest at Lake Alice for the first time. It appears most likely that what the lake offers is an abundance of suitable nest sites sufficiently high above the lake surface, over or surrounded by deep water, and with sufficient twigs for nests. What caused the birds to abandon the other breeding area, Bivin's Arm, is not clear (Mounts, 1949).

During the years 1958, 1959, and 1960 the woody growth of Lake Alice continued to die back; the only remnants of the old hammock being a few huge oak stumps. Most of the buttonbush that was rooted in more than a couple of feet of water was in poor condition and put out only a few new twigs each year. By far the best woody growth in the lake during those years was on the west bar, a shallow bar in the west end of the lake, in other shallow areas near the middle of the south shore, and on the floating islands. There are several floating islands in the southeast bay of Lake Alice. It is on these islands and on the west bar that nearly all of the birds have nested during these three years.

It was on the largest of these floating islands that most of the quantitative data on the breeding ecology of the herons was collected in 1960. The island was anchored by the tree roots and was surrounded by water six or more feet deep. The island raft was composed of living and dead roots, which acted as the principal binding agent, and decayed and

decaying organic matter, which made up the bulk of the substrate. The living plants, especially their roots and tubers, played a most important role in maintaining the integrity of this island. Water pennywort grew over most of the area and was the only ground cover in the heavily wooded portions. A begonia (Begonia semperflorens) grew where there was partial shade, and broadleafed cattail and water willow (Decondon verticillatus) grew in exposed places. The water pennywort grows out over the water for several feet around the edge where it is invaded by water-hyacinth. Lush growths of water-hyacinth marks the positions of ponds and channels which transected the study area. Red maple is the dominant tree and occurs throughout the middle of the island. Button-bush is as numerous but does not attain the size of the red maple and occurs over the entire area, least abundantly around the edges. Wax myrtle is not abundant and is scattered through the middle. Willow grows mostly around the edge of the island where its large, irregular trunks grow out over the water. Elder grows only in maximum sunlight and occurs around the edges.

Ardeidae of Lake Alice

The ardeids that are known to have nested at Lake Alice include: Green Heron, Little Blue Heron, Cattle Egret, Common Egret (Casmerodius albus), Snowy Egret, Louisiana Heron, Black-crowned Night Heron, and the Least Bittern. In addition Glossy Ibis (Plegadis falcinellus) and White Ibis (Eudocimus albus) have nested there. The Anhinga (Anhinga anhinga) also nests in association with the heronry. The Cattle Egret first nested at Lake Alice in 1954 (Rice, 1956), and has nested there each year since. Common Egrets have not nested there since at least

1958, and in 1960 for the first time the White Ibis did not remain at Lake Alice to breed although they did appear early in the spring. Other long-legged wading birds found at Lake Alice, but which are never known to have nested there include Great Blue Heron (Ardea herodias), Yellow-crowned Night Heron (Nyctanassa violacea), and Wood Ibis (Mycteria americana).

During the 1960 breeding season, when the quantitative data on reproduction and food habits were gathered, the populations of the ardeids at Lake Alice were conservatively estimated as: Green Heron, 8 pairs, Little Blue Heron, 225 pairs; Cattle Egret, 300 pairs; Snowy Egret, 275 pairs; Louisiana Heron, 150 pairs; Black-crowned Night Herons, 2 pairs; and Least Bitterns, 12 pairs. Thus there were nearly 2,000 adult ardeids in the heronry during the nesting season. About 200 Glossy Ibis and 2,000 White Ibis roosted at the lake for a few days early in the 1960 season, but only 2 pairs of Glossy Ibis built nests.

A few herons are found in the Gainesville area during the winter. Although there was a winter roost at the east end of Payne's Prairie, these birds roosted primarily at Lake Alice. During the three years, the population began to build up after mid-February, and the adult population reached its peak during April when most nesting was initiated. A few birds fed at Lake Alice until nesting started, but after that the adults no longer fed there. Later, the young fed around the edges of the lake, especially near the heronry, but they continued to be fed by the adults during this period. In the main most of the herons fed on Payne's Prairie from the time they first arrived. One or two birds usually fed at nearby sewage settling ponds. In addition, sinks, small woods marshes, streams, roadside ditches, and other waters are occasionally

visited by foraging herons. When there was a sudden concentration of food at one of these latter places, large numbers of herons congregated there.

As the young started flying and were able to move away from the lake to feed, there was a movement of herons away from the Gainesville area. The increase in the local heron population which must be expected as a result of that season's production, was never more than temporarily attained. Their numbers dwindled during late September and October, and during late November or early December their numbers fluctuated sporadically, probably as the result of southward migration. By mid-December their numbers were greatly reduced and remained lower through the winter than at any other season.

Other Heronries

Although most observations were made at Lake Alice, Payne's Prairie, and elsewhere in the Gainesville area, I studied herons at several other places in Florida during 1958, 1959, and 1960. The more important of these localities are shown in Figure 2. I made repeated observations on the feeding behavior of herons breeding at Orange Lake, Marion County; at Lake Griffin, Lake County; and at Snake and Sea Horse Keys, Levy County. In addition I made three visits into the heronry at Lake Griffin in 1960 and one visit each into the heronries at Lake Butler, Orange County; Lake Okeechobee, Glades County; Tampa Bay, Hillsborough County; and Snake Key, Levy County. Many additional casual observations not included in this report were made at these and other Florida localities outside the breeding season.

Methods

The method employed most was observation, often with binoculars or telescope. Observations of adult behavior throughout the breeding season were made from several vantage points around Lake Alice during 1958, 1959, and 1960. In 1960 detailed observations were made inside the heronry. As each nest was found it was tagged with a number. The tagged nests were visited daily and the condition of the nest, number of eggs, or number of young was recorded. A piece of chrome plated tin was attached at an angle to the end of a ten-foot pole and was used to see into overhead nests. The eggs in nests that were low enough to reach were marked with waterproof ink as they were laid and the fate of each individual egg was followed. Two blinds were placed on the island and were used occasionally.

During the 1960 season a total of at least 495 nests were tagged. There was no way of identifying the owners of these nests at first, but since they were kept under daily observation most of them were eventually identified. However, many of these nests were not completed by the adults, many others were destroyed before the identity of the adults could be determined, and ownership of many nests was not determined until the young hatched. At the end of the season, daily observation had been made on a total of 275 successful, marked, and identified nests. This number included 102 Snowy Egret nests, 85 Cattle Egret nests, 58 Little Blue Heron nests, and 35 Louisiana Heron nests. Observations on practically all of these nests extended from early nest building through rearing of the young.

Observations of feeding adults were made primarily on Payne's Prairie where most of the birds that nested at Lake Alice fed, and although it

was relatively unimportant as a feeding area, at Lake Alice. Study of the herons' food habits was based on the analysis of material obtained from nestlings and older, but still flightless, herons. These young birds regurgitated their last meal when they were disturbed. The amount of disturbance necessary to make them regurgitate varied not only between species, but also between broods. Pellets of identifiable food were preserved immediately in 10 per cent formalin. From one to several days later the pellets were washed and transferred to 30 per cent isopropanol. Later the food items were identified, counted, and their volume determined by absorbing excess water with paper towels and then measuring the volume of water the food displaced. Because of possible distortion, volume is discussed as per cent of total volume. Although many more pellets were collected, the discussion of food in this report is based on the analysis of 50 relatively undigested pellets recovered from young of each of the four herons.

Numerical data are usually presented as mean data. These figures are followed by parenthetical statements of the size of the samples, the range of the observations, and their standard deviations (abbreviated as S.D.). Where it would be redundant, this parenthetical information is not given. The standard deviation is included as a measure of the dispersion of the observations about the mean. The inclusion of these data serve as an indication of the biological significance of the means, and give the reader additional information, and it was urged by Davis (1955) for one, that when available this information always be included.

The "t" test is used to compare two means. In these tests, the hypothesis is made that the two means are equal. The level of significance

is .05. When the hypothesis is rejected, it is assumed that the two means are from different "populations." Statements regarding the significance of the means are accompanied by the "t" values.

REPRODUCTION

One species or several species may nest in a given heronry. When more than one species nests, as at Lake Alice, it is called a mixed heronry. The term rookery, though often applied to heronries, is the name of a place where Rooks (Corvus frugilegus) nest and is not properly applicable to herons. In this chapter the breeding activity of the four most numerous herons at Lake Alice is described. Following the three introductory sections which deal with all four species of herons, are individual accounts in which the statistics of each species are presented.

Winter Status and Spring Arrival

Herons winter in large numbers in south Florida, but are noticeably less abundant along the northern Florida coasts and along the Central Highlands. Although the Gainesville area is marginal as a wintering area for ardeids it is not far distant from acceptable wintering habitat. The abundance of ardeids in the Gainesville region during the winter fluctuates drastically and appears to be related to the weather especially temperature. During December and early January there are fewer birds in the area than at other times. After a few days of lowered temperature, or two or three nights of freezing temperature, practically no Snowy Egrets, Little Blue Herons, or Louisiana Herons can be found. After about a week or ten days of average temperature, or after several days of above average temperature, and later, with the approach of

spring, their numbers gradually increase and mixed flocks of 100 to 300 or more roost at the lake. Present observations indicate that the Cattle Egret is not going to follow this general pattern, but rather will use Lake Alice as a regular winter roost. Through the winter of 1959-1960 approximately 100 Cattle Egrets, and in 1960-1961 approximately 250 Cattle Egrets roosted at Lake Alice. These wintering birds fed in different places than did Cattle Egrets during the breeding season; they followed different local flight paths, and roosted in a part of the lake not used for breeding by any species of heron during the 1958, 1959, or 1960 seasons.

During February, or even as early as late January, the number of herons roosting at Lake Alice begins to increase. There is a gradual build-up until a maximum is reached about the time nesting begins. Throughout this period the birds fly directly to the roost where the individuals remain quiet and seldom move about except for an occasional conflict over a perch. Occasionally a whole group of birds will take flight and move to a different part of the lake to roost, but in the evening later in the season, the individuals are very active when they arrive at the roost.

Onset of Breeding

The first activity which seemed to be related to the onset of breeding was the increased restlessness of roosting birds. In mid-March individuals started flying around within the roosting area. There did not appear to be any directiveness to this new behavior. The birds did not seem to be engaged in any productive effort and their behavior apparently only reflected a general restlessness. Another change at this

time was the return of a few birds to the heronry as early as two hours before sunset, and, in the morning, a few stayed long past the departure of most of the other birds. These individuals perched in the bushes and trees part of the time but spent most of their time "exploring" the heronry, hopping from limb to limb and making short flights from one part of the heronry to another. After only one or two days the males centered their activities around a particular bush or tree and their short flights brought them back to this place. They directed threat displays at every heron that approached them closely, regardless of species. Here they eventually performed the courtship displays. The males did not feed in these areas and had to leave them unoccupied when they left to feed. After pair formation one of the pair always remained in the now established territory.

When they first became more sedentary, the males spent most of their time defending that place by directing threat postures at and attacking other individuals. Although this primarily hostile behavior has sexual implications, the males' behavior changed and became primarily sexual after one to several days of hostile behavior. It is not clear whether this shift in behavior was due to other birds avoiding the area defended by males or to continued development of the males' sexuality, but it was probably brought about by both. The most impressive and most complex sexual display is the Stretch Display, described in detail by Meyerriecks (1960). The male has established his territory when he begins performing the Stretch Displays, but may leave during mid-day and in so doing he runs the risk of losing that territory. The Stretch Display is apparently common to all herons, but there were interesting differences in the way the display was performed by each of the four

species studied. This was the primary sexual display that attracted females. A male of any of these species which performed a series of Stretch Displays with vigor and with bold movements was soon surrounded by a group of his kind (although sexes of the individuals in the group were unknown to the observer later behavior indicated that the group usually included at least one female.) When an individual approached too close, the male interrupted the displays long enough to drive that individual away and then returned to his perch and resumed the Stretch Displays. A female ready for pair formation would repeatedly approach the male and then retreat from him as he came at her in a threatening attitude. The male would eventually not threaten the female and the pair bond was established. Within a few days of pair formation the birds started distinguishing between individuals flying through the territory and those actually invading the territory, and they ignored the transients.

The breeding behavior of herons has been investigated by others and a detailed discussion of their comparative breeding behavior is beyond the scope of this study. Published reports on heron breeding behavior include Meyerriecks' comparison of several species (1960), detailed descriptions of Black-crowned Night Heron behavior by Noble and Schmidt (1938) and by Allen and Mangel (1940), and an exhaustive report on the Gray Heron by Verwey (1930).

Sequence of Nesting

Although most of the birds arrive four to eight weeks before the start of breeding, and there appears to be no substantial difference in the time the four species arrive at Lake Alice, the species do start nesting at slightly different times. Practically all Louisiana Heron

nesting is confined to the early part of the season. In 1960, 94 per cent of all clutches were completed before April 28, most of them during the first two weeks of April. Most Little Blue Heron nesting was also confined to the early part of the season. Sixty-seven per cent of the Little Blue Heron clutches were completed by April 28 but about 30 per cent of the Little Blue Heron clutches were not completed until between mid-May and early July, mostly during the last three weeks of June. Snowy Egrets also started nesting early in the season, but unlike the Louisiana and Little Blue Herons which had completed most of their clutches during the first two weeks of April, the Snowy Egrets completed most of their clutches during the last two weeks of April. Eighty-seven per cent of all of their clutches were completed by April 28, and although a few new nests were built throughout the season, the rate of new nest construction decreased rapidly after the first peak. Cattle Egret nesting started about the time the Snowy Egrets reached their peak, that is about two to three weeks after the other species started nesting, and the Cattle Egrets reached their peak two weeks later than did the Snowy Egrets; 64 per cent of all Cattle Egret clutches being completed by May 12. Additional Cattle Egret clutches were completed throughout the season and there was a second peak of activity during the first half of July. Cattle Egret nesting effort was more equally distributed throughout the season than were nesting efforts of the other species. The last Cattle Egret clutch in the study area was completed July 15. Some were completed even later elsewhere in the heronry.

Snowy Egret

Nest Site

Snowy Egrets built their nests on the sturdiest sites available in the territories which had been established by the males. The first territories established in each new area of the heronry as it expanded during the season were those few areas that included remnants of old nests. Old nests offered especially sturdy places to preen, court, copulate, and eventually nest, and were consequently in great demand by all species of herons. If available in the territory a nest left over from the previous year was used as the base for a new nest.

Next in importance as nest sites were limbs. The main trunk of the tree was used as a support for one side of the nest, and the structure was built out on two limbs.

The third most common nest site was in the basket-like growth that had formed at the stubby end of some trunk as a result of herons breaking off nesting material in previous years. Some species broke twigs off living trees, and when the terminal shoot, especially of wax myrtle, is thus pruned, growth of limbs immediately below that point is stimulated. The result is the basket-like structure which makes a very sturdy nest site. Less exploited nest sites included horizontal limbs such as those commonly used by Little Blue Herons.

The average height at which 96 Snowy Egret nests were built in 1960 was 5.7 feet above the heronry floor or the lake surface (range 3-11 feet, S.D. = 1.33). Snowy Egrets built more of their nests in red maple (43 per cent of all nests in 1960) than in any other tree or bush. Buttonbush was second (26 per cent) in importance and elder, willow, and wax myrtle were used for 18, 7, and 6 per cent of the nests respectively.

The nesting substrate of Snowy Egrets in Florida is described as cypress and mangrove swamps and buttonbush ponds (Howell, 1932) and willow islands (Bent, 1926). Elsewhere they build their nests in red cedar (Wilson in Bent, 1926), prickly pear and huisache and reeds (Bent, 1926). The nests are placed on the lower limbs from 8 to 12 feet above the water (Howell, 1932), in willows of 8 to 15 feet (Bent, 1926); but nests on Vingt-une Island, Texas, were built very close to the ground or at heights up to 5 or 6 feet. In coastal mangrove heronries, such as Snake Key or the Alafia River spoilbanks on the west coast of Florida, the nests were much higher than at Lake Alice and higher than those mentioned in the above reports; the lowest nests were about 8 to 12 feet above the ground.

Nest Building

Nesting material was gathered only by the male and brought to the female who worked it into the nest. When the twig-carrying male was a few feet from the female he elevated his crest, drew his neck into an "s" curve and elevated his aigrettes. The female responded with a similar feather movement, reached out and took the twig in her bill. Both birds immediately sleeked their plumage as the female turned directly to the nest with the twig. As nest building progressed the intensity of this display diminished until the birds no longer elevated the aigrettes, but they usually continued to elevate the crest. The female normally held the stick near the middle. Several efforts were usually needed to push it into the nest, pushing, sometimes getting it part way lodged and pulling it out again, until it was well anchored. The twig was dropped frequently, but the male usually found it on one of his later trips.

All the sticks were gathered from the ground or shallow water beneath the heronry. Howell (1932) commented that Snowy Egret nests are built of dead twigs. The usual pattern followed early in the season before vegetation became rank was for the male to return directly to the ground from the nest and walk around until an acceptable twig was located. Often several were picked up and rejected and on occasion attempts to pick up tree roots or branches of large limbs were observed. The male walked back to the nest tree and climbed up to the nest if there were suitable footholds, otherwise a big hop and a short flight of two or three wingbeats brought him close enough to the nest so that he could pass the twig to the female. Increased growth of vegetation altered this pattern later in the season, and the male had to fly a short distance.

All the twigs in some nests were coated with mud. As the season progressed, females of all species accidentally dropped sticks which they were working into their nests, and some nests were torn apart by the wind or other herons and scattered on the ground beneath the heronry. Fresh twigs, some still with green leaves, became as abundant on the heronry floor as were the old mud-coated ones, and later in the season they were more available than the other twigs. These new twigs were used according to their availability and Snowy Egret nests built later in the season were easily distinguished from older nests.

The pair spent from three to six days, rarely as many as eight days, building the nest before the female started laying; the average for 21 nests was 4.4 days (range 3-8, S.D. = 1.15). Nest building continued through egg-laying, especially the first two or three days, but the nest was usually completed by the time the last egg was laid.

The gradual but continual loss of twigs during incubation was offset by the addition of new material.

Egg Laying and Clutch Size

Snowy Egrets laid their eggs before 9:00 in the morning. The first egg was laid from three to eight days after the adults started building the nest but the nest was seldom completed by then. The first egg often passed down into or through the nest; and occasionally the second egg was lost this way. The second egg was laid an average of 1.8 days after the first egg, and the other intervals were 2.0 days between the second and third eggs, 1.9 days between the third and fourth, and 1.8 days between the fourth and fifth eggs. The over-all average was 1.9 days between eggs (114 intervals, range 1-2 days, S.D. = 0.34). This data is in agreement with Dawson (1915) who on the basis of hatching pattern, concluded that the eggs are laid on alternate days. At Lake Alice the most frequent two-day interval was between the second and third eggs. Intervals of more than two days were not recorded. Typically there was only one, one-day interval per nest, and the fifth egg was the egg most frequently laid one day after its predecessor. The adults spent an average of 7.3 days in egg laying (average number of eggs laid times the average interval).

Snowy Egret clutches at Lake Alice (see Table 1) contained an average of 3.9 eggs (102 clutches, range 2-5, S.D. = 0.67). Howell (1932) reports the clutch as three or four, but Bent (1926) says the clutch is ordinarily four or five, sometimes only three and rarely six. Early clutches, that is those completed between April 4 and April 28, averaged 4.1 eggs (89 clutches, range 3-5, S.D. = 0.48), but late nests contained substantially fewer eggs. Clutches completed between April

Table 1.--Frequency Distribution of Clutch Size of Snowy Egrets, Lake Alice, 1960

	Clutch Size			
	2	3	4	5
All nests	3	15	69	15
April 4 to April 28	0	7	67	15
April 29 to June 16	3	8	2	0

29 and June 16 averaged 2.9 eggs (13 clutches, range 2-4, S.D. = 0.62). These late nests are probably all renesting attempts of birds whose earlier attempts failed. The difference between the means of the early and late clutches is significant at the .01 level ("t" = 7.79).

The average number of eggs laid in nests that eventually contained complete clutches was 4.1 (100 nests, range 2-8, S.D. = 0.64), but some eggs were lost before the clutch was completed and additional eggs were certainly lost before they were recorded.

There is no evidence that any of the Snowy Egrets raised two broods at Lake Alice. The nesting season is sufficiently long for raising two broods, but nesting activity decreased rapidly and continuously after the initial peak, and there was no evidence of a late second peak of activity. At least one brood of two young was raised from the age of a few days by only a single parent at Lake Alice during 1960, and it might be reasoned that one parent could be relieved from care of the first brood and start a second. However, even nest building behavior demands two birds: a male to hunt twigs and deliver them to the nest site and a female to take the twigs and fashion a nest from them. Protecting a nest against depredations of other nest building herons and protecting the eggs from predators also require the presence of two individuals.

Incubation

Snowy Egrets usually started incubating the day after the second egg was laid, or sometimes they started the day the third egg was laid. Although there was considerable variation, the adults seldom incubated one egg, sometimes incubated two eggs, but always started incubating

by the time the clutch contained three eggs. The pattern of hatching of the young indicates that effective incubation may actually have begun somewhat earlier than observations of adult behavior indicated. These observations conflict with Dawson's (1915) statement that, on the basis of hatching pattern in three nests, incubation starts with the laying of the first egg.

The incubation period averaged 22.4 days (39 nests, range 21-24 days, S.D. = 0.75). The most frequent incubation periods were 23 and 24 days with 21 and 12 observations respectively. Three nests hatched in 22 days. The incubation period of 18 days reported by McIlhenney (1912) is the only one quoted by Bent (1926), and is the figure given by Sprunt and Chamberlain (1949). Eighteen days is approximately the duration from the laying of the last egg to the hatching of the first young at Lake Alice. At Lake Alice both sexes incubate, and Bent (1926) has reported this for other localities. Although the Snowy Egret nest is an open network of twigs offering little protection from below against cold or wind, there appears to be no correlation between clutch size or weather and length of incubation period. The nest is important to the adults for several activities, but all it offers the eggs is protection from falling to the ground.

Hatching and the Young

The chicks could usually be heard calling inside the egg for two or more days before they pipped. The young may hatch completely in less than 24 hours, but most young pipped at least one day before they hatched. The young are covered with a moderate amount of white down which dries in a short time.

On the first day of hatching, the nests contained one or two, rarely three chicks, and they averaged 1.5 (80 nests, range 1-3, S.D. = 0.62). The second day of hatching most nests contained two or three chicks, a few contained one, and about half as many contained four as contained one. They averaged 2.4 chicks the second day (68 nests, range 1-4, S.D. = 0.76), an average of nearly one per nest hatched between the first and second day. About half the nests had three on the third day and most of the others had two or four. They averaged 2.9 chicks on the third day (59 nests, range 1-4, S.D. = 0.85). However Dawson (1915) found three nests in California in which the young hatched on alternate days, a sequence not observed at Lake Alice.

An average of 3.3 young hatched per nest (91 nests, range 1-5, S.D. = 0.96). It took an average of 3.2 days (75 nests, range 1-6, S.D. = 1.14) for all to hatch. The hatchlings were able to lift their heads for only a moment at a time during the first two days. On the third day they could keep the head elevated for considerable time and were often heard peeping. After a few days they became silent when disturbed.

The parents brooded the young for several days, one parent nearly always on the nest. Bent (1926) reported that both adults care for the young, but one of them always remains at the nest. At Lake Alice especially during mid-day and in June and July broods, the adults spent much of their time standing over the young shading them. McIlhenny (1912) provides an excellent photograph of an adult shading young. Both parents feed the young, but until the young were old enough to hold their heads up and strike at foreign objects that came to the nest, one of the parents always stayed at the nest while the other hunted and

brought food to the chicks. After the young were about one week to 10 days old, the parents no longer stayed on the nest through the day. After this time both parents started hunting and bringing food to the young at the same time.

At first the young picked food off the floor of the nest where it had been regurgitated by the adults. After a few days, they quickly passed through a stage of taking the food from the parents' bills, the several young grabbing for the bill at one time. The young next progressed to the procedure of sticking their heads into the bill and mouth, reaching down into the throat and intercepting the regurgitated food on its way up. In broods that hatched over a period of several days the oldest young might thus be taking fish out of its parents' throat while its youngest sibling was still too weak to hold its head up.

Mortality of Eggs and Young

The loss of eggs from nests between the time of laying and the start of hatching was at least 5.4 per cent. During the hatching process there was a mortality of 14.7 per cent. From egg laying through hatching there was an over-all minimum mortality of 19.3 per cent.

The average number of hatchlings surviving until two days after the last young hatched was 3.0 (86 broods, range 1-5, S.D. = 0.97), this is significantly fewer than hatched ("t" = 1.67). The brood size was reduced still further to an average of 2.7 chicks by seven days after hatching (77 broods, range 1-5, S.D. = 0.86), and two weeks after the last young hatched, an average of only 2.2 young survived per nest (65 broods, range 1-4, S.D. = 0.84). These losses are greater than those of the first two days. After two weeks the first hatchlings were often able to leave the nest and later estimates of mortality are

unreliable. The reduced number of observations of older broods is due in part to intentional termination of observations at some nests. The total mortality during the first two weeks of nest life was 32.6 per cent. The over-all loss exceeded an average of one chick per nest; of the 3.3 that hatched, an average of 2.2 chicks per nest survived for two weeks. Practically all this loss was due to starvation. The last chick to hatch was considerably behind the earlier ones in development and size and was incapable of successfully competing with four siblings and often incapable of competing with three. As each day passed the older nest mates developed and grew while the youngest waned until eventually it died of starvation.

Nests that contained four chicks two days after hatching had an average of only 2.5 chicks two weeks after hatching. Broods that contained three chicks two days after hatching were reduced to an average of 2.3 by the end of their second week, and broods of two were similarly but much less drastically reduced to 1.8 checks. Thus 1.5 young were lost from broods of four, 0.7 were lost from broods of three, and less than 0.3 were lost from broods of two. It appears that the adults were able to feed and raise a maximum of about 2.5 young per nest. Of the 31 nests in which four or more young hatched, only two nests held as many as four two weeks later. The young that starved were usually trampled into the nest by their siblings, but were occasionally ejected from the nest. The minimum over-all loss of both eggs and young from egg laying through the first two weeks of nest life was 45.6 per cent.

There was a sharp increase in mortality when the young first left the nest and started climbing around in the bushes and trees. At Lake

Alice the trees and bushes were short and scrubby, and those young who fell to the ground were usually, but not always, able to get back to their nests. The young were extremely agile and used their heads and necks as prehensile aids in climbing. Nevertheless, during 1960 I found two large juveniles hanging dead. One was upside down with the foot caught and the other was caught by the wing. Young that wandered into the nest site of nearby birds were attacked, especially if the neighbor was a Cattle Egret, and were driven or knocked from the tree.

Cattle Egret

Nest Site

Old nests were seldom available in Cattle Egret territories because other species had already established territories to include the old nests before the Cattle Egrets started nesting. But Cattle Egrets occasionally built on top of a nest formed earlier in the season by some other heron and later abandoned by it. Some of the Cattle Egrets which started nesting as late as June or July were able to use nests recently abandoned by young Snowy Egrets or Little Blue Herons. Cattle Egrets were the last to breed and generally acquired territories and nest sites higher in trees and bushes than did the other species. As a result there was less stable support for their nests. Heron territories at Lake Alice had definite vertical as well as lateral limits. The most favored nest site appeared to be in the basket-like growth of limbs which resulted from the breaking off of terminal twigs for nest material in previous years. Cattle Egret nests were often built against the tree trunk on a pair of small limbs, in

the fork of a horizontal limb, which gave support in three directions from the nest center; or between the two branches just beyond the fork. These nests were quite stable. Another frequent site was on a cross formed by two limbs, often where a dead tree had fallen over on a live one.

The average height of 76 Cattle Egret nests in 1960 was 7.8 feet (76 nests, range 5.5-12.0, S.D. = 1.39). Many of their nests were placed in either red maple (33 per cent of all nests) or in buttonbush (29 per cent). Elder was also used frequently (19 per cent of the nests) and wax myrtle and willow were used least (12 and 7 per cent, respectively).

Cattle Egrets breed in a variety of sites throughout their extensive range. This species builds its nests in reed beds in East Africa (Mackworth-Praed and Grant, 1957) and from 50 to 80 feet up in eucalyptus trees in South Africa (Skead, 1956). Whistler (1949) says that in India they often nest at considerable heights. However, in Africa and India and throughout their range they most commonly nest at less than 20 feet. In Japan they nest 10 to 20 feet from the ground in the low branches of trees, shrubs, or bamboos (Austin and Kuroda, 1953), and in their generalization Witherby et al. (1947), say Cattle Egrets usually nest in trees and bushes growing in water but that they also nest in big cork-oaks on dry ground, on rocky islets, and in big trees in towns in Egypt.

Nest Building

Nest material was brought to the females by the males. This was the typical sequence: the male landed near the female, stretched his neck, and proffered the twig to the female; the male usually landed quite close to the nest but sometimes had to take a step or two, or

hop down one more limb, before passing the twig. The male elevated the crown and back feathers and sometimes the chin feathers as he offered the twig; the female elevated her feathers, took the twig, sleeked her plumage as did the male, turned to the nest, and pushed the twig into the nest. The female laid the first few twigs in a little pile, but worked later twigs into the nest by trial and error. She accidentally dropped many. Although Witherby et al. (1947) say that both sexes build the nest, Skead (1956) says that one bird gathers the nesting material, but the other does the actual building, my observations confirming the latter.

The male flew directly to the upper parts of trees and bushes after delivering a twig to the female. He broke off twigs, but unlike the Snowy Egret never descended to the heronry floor to pick up twigs lying there. Skead (1956) says that in South Africa they gather material from the ground or pull it from the trees. The dead, brittle twigs were broken off by the earliest nesting Cattle Egrets and Little Blue Herons. The twigs broken off by later nesting individuals were live and tough. The male spent much time looking for a twig he could reach. He would grab it in his bill, pull back on it, jerk it, pull back, lean back precariously flapping with his wings, recover his perch, give it another jerk, and often fail to break it off.

At first the males gathered twigs from the bushes and trees within the heronry. They soon exhausted this supply, and started foraging farther from the nest site. By mid-season, Cattle Egrets were gathering twigs from bushes and trees around the lakeshore and from distant parts of the lake. Late in the 1960 season a few males gathered sticks more than a half mile south of Lake Alice and flew back to the lake with them. The birds gathered a few twigs about the heronry throughout the season as the vegetation continued to grow.

Nest building continued for an average of 6.6 days (26 nests, range 3-11 days, S.D. = 1.88) before the first egg was laid. There was considerable variation in the rate at which sticks were added to the nest. In some nests a few sticks were gathered and nothing more was added for several days, while in others the bulk of the nest was completed within two or three days. The adults continued to add a few twigs to the nest during early incubation; nests were essentially complete early in the egg-laying period, and subsequent twigs were added for repair and maintenance of the nest.

If one member of each pair was not always present at the nest throughout and following construction other herons, which were always on the prowl for nest twigs, dismantled the nest. Many birds added substantially to their nests every day up to egg laying. A few birds completed their nests several days before the female laid the first egg.

Egg Laying and Clutch Size

Cattle Egret nests were fairly complete when the females laid their first eggs, and they seldom lost these first eggs because of poor nest construction. The eggs were typically laid before 9:00 in the morning. The interval between egg laying was two days; the interval was determined between the first and second eggs 29 times, second and third eggs 38 times, third and fourth eggs 20 times, and fourth and fifth eggs 2 times.

The clutches averaged 3.5 eggs (85 clutches, range 1-6, S.D. = 0.69). The number of eggs in each nest is summarized in Table 2. Clutches completed between mid-April and mid-May averaged 3.6 eggs (64 clutches, range 3-5, S.D. = 0.58), and those completed between mid-May and mid-July averaged 3.4 eggs (31 clutches, range 1-6, S.D. = 0.99).

The late clutches thus are both slightly smaller in average size and slightly more variable in size (see also Table 2), however they are not significantly smaller ("t" = 0.84). Cattle Egret clutch size appears to vary throughout its range, it is given as: three to five in Japan (Austin and Kuroda, 1953), one to three in East Africa, three to five in South Africa (Mackworth-Praed and Grant, 1957), two or three in South Africa (Skead, 1956), four or five in India (Whistler, 1949), and four or five, six occasionally, is given as a generalization by Witherby et al. (1957).

Late broods were not smaller than the early ones. There was no evidence that any of the Cattle Egrets raised two broods. Although nesting extended over a long enough period to allow a few of the earliest to nest again, very few pairs did nest at the end of the season, and they were more likely pairs which started late in the first place and failed with their first attempts.

Incubation

Incubation at Lake Alice, as in South Africa (Skead, 1956), was by both sexes. Observations indicate that incubation began in all nests with the first egg. Typically however, one young hatched in each nest the first day. The second day a second one hatched in about half the nests. Since the second egg was always laid two days after the first, it follows that if incubation started when the first egg was laid the second egg should have hatched two days after the first. Effective incubation apparently began the day the first egg was laid in about half the nests, and the day after the first egg was laid in the other half. This was probably delayed in many nests because the adults spent much of the first day adding twigs to the nest.

Table 2.--Frequency Distribution of Clutch Size of Cattle Egrets, Lake Alice, 1960

	Clutch Size					
	1	2	3	4	5	6
Total number of nests	1	3	41	33	6	1
April 15 to May 12	0	0	28	22	4	0
May 13 to July 15	1	3	13	11	2	1

The average incubation period of the Cattle Egret was 22.9 days (30 nests, range 22-23, S.D. = 0.24). Incubation was 22 days in two clutches and in the remaining 28 nests required 23 days. According to Witherby et al. (1947) the incubation period is 21-24 days. Skead (1956) gave the incubation period as 26 days, which would be about the time from the laying of the first egg to the hatching of the last young in clutches of two or three which he observed.

Hatching and the Young

The young could be heard calling inside the egg for a day or two before they hatched. They often pipped the day before they hatched. Sometimes they pipped two, or rarely three, days before hatching. The young dried off rapidly. They were covered with a moderate amount of white down, and had a fairly well pronounced crown.

The first day of hatching the Cattle Egret nests averaged 1.1 young (49 nests, range 1-2, S.D. = 0.28); 45 of 49 nests contained one and the other four nests held two chicks each. The second day of hatching the nests averaged 1.6 young (41 broods, range 1-3, S.D. = 0.58); they averaged 2.1 on the third, 2.6 on the fourth, and 3.0 on the fifth day. In general terms, the nests averaged one chick the first day and increased at an average rate of one every other day thereafter. This correlates with the rate at which the eggs were laid. About half the first-laid eggs hatched one day before, and half hatched two days before the second egg hatched, but all later eggs hatched one every other day.

An average of 3.2 young hatched per nest (73 nests, range 1-5, S.D. = 0.81). The average hatching time was 4.7 days per nest (41 nests, range 1-8 days, S.D. = 1.83). The adults continued to brood the young for several days after hatching started. Skead (1956) also noticed that

there was little change in adult behavior when the young first hatched. In many nests the last young hatched seven or even eight days after the first one, and the adults were not able to incubate continuously during the day for that period of time because the oldest siblings were large and required considerable food. The combination of high air temperature and large siblings was obviously sufficient to provide warmth to carry the eggs through the last few days of incubation. The "peck-order" that Skead (1956) noted in Cattle Egret broods was probably the simple dominance of larger over smaller nestlings. During mid-day brooding of the young chicks and eggs consisted mostly of shading them in practically all the late nests. The parent stood over the nest with the body at a right angle to the sun's rays, often with the wing nearest the sun drooped and shading the young.

At first the young were too weak to do more than lift their heads momentarily. They spent their time resting and picking food up from the floor of the nest. After a few days they could hold their heads up and take food directly from the parent's bill. From this time on they spent most of the daylight hours sitting up in the nest with the wings partly extended, the bill open, and the gular pouch fluttering. As with the Snowy Egret, the young were soon able to reach down into the parent's gullet and remove food before the parent could regurgitate it.

Mortality of Eggs and Young

Adult Cattle Egrets were extremely attentive and seldom lost any eggs from their nests. From egg laying to the day before hatching mortality was only 3.9 per cent. Occasionally a predator took all the eggs from a Cattle Egret nest, but these nests could have been ones that had been abandoned already, or the adults might have abandoned

them when they did lose an egg to a predator. Very few clutches were so lost. The hatching mortality was 7.0 per cent, and the minimum over-all mortality of eggs from laying through hatching was 10.7 per cent.

There was little loss of nestlings (2.5 per cent) during the first two days that followed the hatching of the last individual. The brood was reduced to 3.0 young (66 broods, range 1-4, S.D. = 0.79) at the end of the first week, and further reduced to 2.9 young (52 broods, range 1-4, S.D. = 0.80) by the time the youngest chick was two weeks old. The differences between the numbers alive at hatching, two days later, one week later, and two weeks later are not significantly different, but the number alive two weeks after hatching is significantly less than the number hatching ("t" = 1.78). The mortality of nestlings during their first two weeks was 8.2 per cent. The minimum mortality from egg laying through two weeks of age for the youngest nestling was 17.9 per cent.

There was considerable loss of young when they started climbing around in the trees. If they climbed into the nest of an incubating Cattle Egret they were pecked until they left or fell from the tree. Although I never saw the adults kill a young bird, I occasionally saw blood on the young, especially their wings, after such encounters. The nesting vegetation was low and dense at Lake Alice, and young Cattle Egrets that fell to the ground were usually able to get back to their nests. Those that wandered about before attempting to return to the trees frequently fell prey to alligators. In South Africa, young Cattle Egrets that fell to the ground were unable to get back to their nests (50 feet and higher) and starved (Skead, 1956). In 1960, at least five

young Cattle Egrets between three and four weeks old were eaten by alligators around one small pond in part of the Lake Alice heronry. Skead (1956) says that in South Africa "eagles" take the young and "cause great consternation in the colonies." Another unusual cause of mortality was the paralysis of many nestlings which occurred only during one year in the heronry which Skead (1956) observed.

Little Blue Heron

Nest Site

Little Blue Herons built their nests in the territories established by the male, and they usually built them on the perch he had used for courtship. The favored site for both courtship and nest building was an old nest. However, Meanley (1955) says the Little Blue Herons he studied did not use the old nests that were available. At Lake Alice Little Blue Herons were often the first birds to move into and breed in previously unoccupied parts of the lake. The males moved into these areas, established territories that included the few nests of the previous year, using them as platforms where they performed their stretch displays, and preened. Those unable to find such favored sites usually built their nests on small horizontal limbs wedging it against the main trunk. Less common nest sites included forks of large horizontal limbs, places where two branches crossed, or some place where they could lodge the first few twigs.

The average height of Little Blue Heron nests in 1960 was 7.2 feet (49 nests, range 4.5-10.5, S.D. = 1.41). However, Little Blue Herons had two distinct peaks of nesting activity in 1960: in the early peak, clutches completed before April 28, the average nest height was 6.7

feet; in the later period, most clutches completed between June 10 and June 30, the average nest height was 8.5 feet. Little Blue Herons showed strong nest site preferences; they built 49 per cent of their nests in red maple and 36 per cent in buttonbush. They built few nests in elder (11 per cent) or willow (4 per cent) and built no nests in wax myrtle.

According to Howell (1932) Little Blue Herons build their nests in willow, wax myrtle, and, in northern Florida, in titi (Howell, 1932). Willows and other bushes (Bent, 1926), buttonbush and swamp privet are used in Arkansas (Meanley, 1955). Box elder, water maple, overcup oak, and elm are sites in Tennessee (Ganier, 1960), and nests are built in catalpa in Oklahoma (Tomer, 1955). Most of the nest sites just described are over water or on islands, but the catalpa tree heronry in Oklahoma was on dry land. Bent (1926) says that on the willow islands of the upper St. Johns River in Florida the Little Blue Herons nest in bushes on the outer edges of the islands, from two to four feet above the ground. Howell (1932) says the nests are built from four to eight feet above water. In the woods described by Ganier, most nests were between 16 and 25 feet up. In Arkansas Little Blue Herons build their nests closer to the shore than do the other species, and build them at an average height of eight feet (range 3-15 feet) with other nests placed up to 25 feet (Meanley, 1955). In the catalpa woods they nested 9-18 feet above the ground (Tomer, 1955).

Nest Building

The males gathered the nesting material, twigs and small branches, and brought it to the females who built the nests, and Meanley (1955)

reported the males gathering sticks and passing them to the females in Arkansas. At Lake Alice the male flew to nest, and landed close enough to it that he could pass the twig to the female. The male lowered the head, extended the neck, and pointed his bill toward the female who reached out and took the twig in her bill. The male usually turned around immediately and left, but would sometimes remain near the nest and preen or would sometimes move over into the nest with the female. The female turned to the nest with the twig, and if the nest was just being started she would lay the twig on top of the others. If the nest was nearly complete she pushed the twig into the nest from the side. While working twigs into the nest, she frequently dropped them, and at the peak of building the ground beneath Little Blue Heron nests was often littered with twigs.

The male collected nest material by breaking twigs off bushes and trees. Male Little Blue Herons collected twigs at all levels throughout the heronry, but primarily from the upper halves of the trees and bushes. In Arkansas, Meanley (1955) found they occasionally break off twigs, but usually gather twigs from the shallow water beneath the nest. At Lake Alice the males few from tree to tree, grabbing, pulling, shaking, and attempting to break off any one of several twigs before successfully getting one. Each flew directly to his territory with the twig, landed near and usually above the nest, hopped down to the nest, and passed the twig to the female. Because Little Blue Herons nested earlier than the Cattle Egrets, practically all their nests were complete before twigs became scarce, and the males were able to gather all their nesting material in the general vicinity of their own territory. As they wandered about searching for nesting materials, the males took twigs from any

nests that were left unguarded by other birds. Only a few twigs could be pulled from any nest before the whole thing came apart and fell to the ground.

Nest construction continued into the egg-laying period but was generally completed by the time incubation started. The bulk of the material was added to the nest before the first egg was laid. The adults worked on the nest for 4.8 days (12 nests, range 3-8, S.D. = 1.41). Meanley's (1955) statement that nest construction requires, "three to five days, occasionally six or seven days," falls within the range for the Lake Alice birds. Nests were built fairly rapidly at a rather uniform rate, but the birds occasionally had to abandon one site in favor of another a foot or two distant because the place first selected offered an inadequate base for the nest. The first egg was often laid in a very small nest, and in such cases the nest was usually completed with two more days of building. Most nests were obviously "completed" on the third or fourth day. Sticks added later merely reinforced the structure.

Egg Laying and Clutch Size

The female Little Blue Heron laid the first egg from three to eight days after starting the nest. Although a small proportion of nests were not complete at that time, eggs were lost through the nest only occasionally. The eggs typically were laid before 9:00 in the morning. They were laid at a rate of one every 1.7 days (48 intervals, range 1-2 days, S.D. = 0.47). The interval between laying the first and the second egg was 1.7 days, the interval between the second and third egg was 1.7 days, and the interval between the third and fourth egg was 1.7 days.

There was one interval of one day in 12 of the 18 nests that eventually held three or four eggs, in the other six nests all intervals were two days, and in one nest with five eggs the intervals between the first and second and the fourth and fifth eggs were one day. Meanley (1955) seems to have noted that eggs are sometimes laid on consecutive days and not always on alternate days because he says that they are, "deposited on an average of one nearly every other day."

The clutches contained an average of 3.7 eggs (58 nests, range 2-5, S.D. = 0.73). An average of at least 3.8 (56 nests, range 2-6, S.D. = 0.69) eggs were laid in nests that eventually held complete clutches, but some were lost before incubation started. The number of eggs in each clutch is summarized in Table 3. According to Bent (1926) the Little Blue Heron usually lays four or five eggs, sometimes only three and occasionally six, and according to Howell (1932) they usually lay four or five eggs. Meanley (1955) gives an average of 4.04 eggs for 50 nests with a range of from three to five eggs. Few Little Blue Heron clutches were completed between April 26 and May 21, 1960, any place in the heronry, and there was no new nesting activity in the study area during this period. Clutches completed earlier, from April 3 to April 26, averaged 4.1 eggs (39 clutches, range 3-5, S.D. = 0.48). Clutches completed between May 21 and July 4 averaged 2.9 eggs (19 clutches, range 2-4, S.D. = 0.45). This difference is also seen in Table 3. The late clutches were significantly smaller, "t" = 9.07. The reasons why there were no new nesting efforts for a three-week period are vague. The small size of the late clutches is common to many species and was discussed by Lack (1954), and although the adults brought different food to their nestlings after mid-June, the

Table 3.--Frequency Distribution of Clutch Size of Little Blue Herons, Lake Alice, 1960

	Clutch Size			
	2	3	4	5
Total nest for the season	3	18	31	6
April 1 to April 28	0	3	30	6
April 29 to July 4	3	15	1	0

explanation for the smaller clutches is unknown. Most of these late nesting efforts were apparently renesting efforts.

It is highly improbable that Little Herons raised two broods at Lake Alice. A few late nest efforts were started about the time the parents of the earliest broods finished feeding their young. Chronologically it was barely possible, but it is not likely that only the few pairs nesting earliest might raise a second brood, and that they could do so immediately after the first brood became independent. There were more early nesting efforts interrupted than were there late nesting efforts started.

Incubation

In many nests the first egg laid was the only egg which opened on the first day of hatching; but by the second day of hatching three eggs had usually hatched. It appears then that incubation started the day after the second egg was laid or the day the third egg was laid. Adult behavior at the nest indicated that they did not begin to incubate until after there were two eggs in the nest, and that they nearly always were incubating a nest with three eggs. These observations agree with Meanley's (1955) observation that incubation virtually always begins after the laying of the second egg. At Lake Alice, however, the frequent hatching of the first egg one day before the others indicates that it had received at least one more day of effective incubation than had any of the others.

The incubation period for 19 clutches averaged 22.8 days (range 22-25 days, S.D. = 0.73). Eight clutches had an incubation period of 22 days, eight had a period of 23 days, one took 4 days, and two clutches

required 25 days. The two clutches that required 25 days were the only five-egg clutches for which I obtained incubation periods; but there appears to be no correlation between clutch size and duration of incubation.

Both parents incubated the eggs. Published incubation periods agree with the Lake Alice data, Meanley (1955) saying that incubation is done by both sexes and is 22 to 24 days, 22 or 23 days is the rule, and Sprunt and Chamberlain (1949) give the incubation period as 21 to 23 days.

Hatching and the Young

The young called in the egg for a day or two before they hatched. They usually pipped one day before they hatched. However, they occasionally hatched the same day they first pipped, and rarely pipped two or three days before hatching. The young dried shortly after hatching as did young of the other species. They are covered with a moderate amount of down which is white except for the short crest which is a dingy, pale brown.

The first day of hatching most nests contained one young, some had two, and a very few had three. The first day the nests averaged 1.6 chicks (37 nests, range 1-3, S.D. = 0.69). The second day most nests had three, a few still had one or two and a very few had four; the nests averaged 2.5 young (33 broods, range 1-4, S.D. = 0.95). The third day the frequency of nests with four increased and the broods averaged 2.9.

An average of 3.2 Little Blue Herons hatched per nest (51 nests, range 1-5, S.D. = 1.00). Hatching of the entire brood required an average of 3.2 days (31 nests, range 1-7, S.D. = 1.42). The young were weak

and inactive for the first few days, and were unable to raise their heads more than briefly. Within a few days they could hold their heads up for long periods, and called frequently. The adults continued brooding until the young could hold themselves upright. The most obvious change in adult behavior at hatching was an increased restlessness, some individuals stood up and looked at the young, moving around a great deal. Others changed behavior but little. The young first fed by picking up food the adults regurgitated into the nest, but later took food from the adult's bill, and at about 10 to 14 days reached down into the adult's gullet for the food.

Mortality

Little Blue Herons lost few eggs once they started incubation. The mortality from egg laying until just before hatching was 3.9 per cent. There was a loss of 12.1 per cent during hatching. The total mortality from egg laying through hatching exceeded 15.6 per cent. Meanley (1955) does not give comparable data for the Arkansas heronry he studied, but he says that robbing the nests of sticks by other herons and egrets is the principal cause of egg loss.

Although an average of 3.2 eggs hatched per nest, there were only 3.0 young per nest two days after the last egg hatched (47 nests, range 1-5, S.D. = 0.91). This is not significantly less than the number at two days ("t" = 0.98), and they were still further reduced to an average of 2.4 by the end of the second week (40 nests, range 1-4, S.D. = 0.76), the difference between the last two figures is significant ("t" = 2.17). Some of the young started leaving the nest at this time. An average of nearly one young per nest (0.8 young, 47 nests, range 0-4, S.D. = 0.65)

was lost during the two weeks following hatching. The nestling mortality was 26.2 per cent. Practically all these losses were due to starvation of the smallest and youngest hatchlings. Young that hatched as late as four or five days after the first young had hatched seldom developed rapidly enough to be able to successfully compete with their older siblings. Of 30 Little Blue Heron nests that lost young, 23 nests lost one, and 6 nests lost two, and 1 lost four. Meanley (1955) says that their nest mates push them out. He also implicates raccoons, house cats and Black Vultures as predators, none of which appeared to be so at Lake Alice.

Causes of high mortality that occurred when the young left the nest were difficult to evaluate. Most of those that fell out of the trees were able to get back into them. The day after an extremely heavy rainfall, (3.55 inches on June 18, 1960) I found two nearly dead young on the floor of the heronry. Their feathers were wet and packed with mud and their wing feathers had been pounded into the mud by the rain. The next day they were gone and had not returned to the nest tree. One chick about three weeks old was attacked by nearby adult herons of several species when it invaded their nesting territories. It was bleeding on the wing and back and appeared to be very weakened; and it disappeared during the next night.

Louisiana Heron

Nest Site

Louisiana Herons also built their nests in the territories established by the males. It was usually placed where the male held his courtship displays. This is probably because the male selected the

steadiest site available within the territory. The nest site was often an old nest if one occurred in the territory. Such relatively scarce sites were preferred by most other herons at Lake Alice. However, the Louisiana Heron was the first species to start nesting and established its territories to include most of the few old nest platforms available. Birds renesting later in the season were often able to take over abandoned nests. If the territory did not include an old nest, they usually built in the sturdiest place available. Louisiana Herons established territories with comparatively secure perches and seldom lost nests.

The average height of Louisiana Heron nests in 1960 was 5.7 feet (30 nests, range 3.5-7.5, S.D. = 0.96). Louisiana Herons built 39 per cent of their nests in elder. They also nested frequently in buttonbush (29 per cent) and in myrtle (18 per cent of all nests) but they seldom nested in red maple, or willow (11 and 7 per cent, respectively).

In Florida, Louisiana Herons are said to nest in willows, mangroves, buttonwoods, and rushes (Bent, 1926, Howell, 1932). In Texas, Bent (1926) records them nesting in these, and also in cane, mesquite, huisache, and occasionally in prickly pear. The nest height in one Texas heronry is given as one to two feet; and in another heronry as 10 to 15 feet (Bent, 1926). Howell (1932) gives the nest height of Florida birds as 2 to 20 feet, but on the upper St. Johns River Bent (1926) says they build their nests in the middle of the heronries at heights of 2 to 12 feet, and in the Cuthbert Lake heronry they build their nests throughout the heronry at 6 to 12 feet above the ground.

Nest Building

Nesting material was gathered and brought to the female by the male. When returning with nesting materials the male alighted next to the nest and usually a little above it. As he settled to the perch and folded his wings he elevated his aigrettes and offered the twig to the female. She elevated her aigrettes as the male landed, and took the twig from him. They both then lowered their aigrettes. The male occasionally remained at the nest to preen and rest before going after more twigs. The female immediately turned to the nest with the twig, and by trial and error usually found a place for it. Huxley (notes quoted in Bent, 1926) says that in Louisiana, the male "usually, perhaps always," finds the sticks, and the female does the actual building.

Early in the season, nesting material was gathered from the ground beneath the heronry. The male usually picked up dead twigs, and often several were picked up and rejected before one was carried to the nest site. He occasionally broke twigs off large fallen limbs and small bushes and would wander quite far from the territory in this search. After passing the twig to the female he immediately searched for other twigs, and having found a good place to gather them would fly directly to that spot from the nest. Late nests included twigs with fresh leaves. These could have been broken off by the male, or they could have been wastage from nests of other species, which was not determined.

Nest construction was a continuing affair with Louisiana Herons, but the bulk of construction occurred during a period of four to six days, (occasionally up to eight days early in the season, or later as

short as three days). Usually five days passed before the eggs were laid. The male brought the bulk of the nest material during the first three days. By the end of the third day most nests were nearly of their maximal size. The birds added fewer sticks to the nest during the next two days. During this time the nest became more compact as they worked the twigs into the nest structure, and it acquired a more bowl-like shape. The adults continued to add to the nest during egg laying and incubation, but the amount of material brought in waned as incubation progressed. A bird might grab a nest twig and jiggle it or force it farther into the nest whenever it was on the nest.

Egg Laying and Clutch Size

Louisiana Herons laid the first egg about four or five days after the nest was started. The nest was large and nearly complete by this time. Eggs were laid before 9:00 in the morning. The average interval between laying was 1.7 days (40 intervals, range 1-2 days, S.D. = 0.65). The first and second eggs were laid on consecutive days about half the time and on alternate days about half the time (average 1.6 days), but the frequency of two-day intervals increased with each successive egg. The average interval was 1.7 days between the second and third eggs and 1.8 days between the third and fourth.

The Louisiana Heron clutches averaged 4.1 eggs (35 nests, range 3-6, S.D. = 0.66). A few eggs were lost before incubation started and an average of at least 4.3 eggs were laid (35 nests, range 3-9, S.D. = 1.04). The number of eggs in each clutch is shown in Table 4. Howell (1932) gives the clutch as three to five which agrees well with the Lake Alice data, but Bent (1926) says they "usually lay four or five

Table 4.--Frequency Distribution of Clutch Size of Louisiana Herons, Lake Alice, 1960

	Clutch Size			
	3	4	5	6
Total nests	4	22	9	1

eggs, sometimes three, occasionally six or very rarely seven" which is more than they lay at Lake Alice. There was an indication that late clutches at Lake Alice tended to be smaller, but only a few late nests were found, not enough to permit any generalization. The Louisiana Heron was the first ardeid to start nesting, and a high per cent of its early nests were successful. Egg laying was finished in 33 of 35 nests by April 27. The two late clutches were finished May 2 and May 20. Louisiana Herons did not raise two broods.

Incubation

Louisiana Herons at Lake Alice seldom incubated one or two eggs, but were usually incubating when the nest held three or more eggs. The start of incubation, which was variable for all four species, was most variable in the Louisiana Heron. The first day of hatching a few nests contained three young. In some clutches only one chick hatched on the first day, and in a few of these the pattern of hatching indicated that incubation started the day before the second egg was laid. In clutches of five eggs there were usually four chicks by the third day of hatching, and most of those that did not have four had three. Incubation most frequently started the day before the penultimate egg was laid.

The incubation period for 10 clutches averaged 23.8 days (range 23-25 days, S.D. = 0.60). Three clutches hatched in 23 days, six clutches in 24 days, and one took 25 days. The 25 day clutch contained five eggs as did two of the 24 day clutches, but no conclusions can be drawn from the data. The widely given incubation period of 21 days is credited to Audubon (1840) by Bent (1926). Both parents incubated.

Hatching and the Young

The young called inside the egg for a day or two before they hatched. Typically they pipped the day before they hatched. The adults dropped the empty shells over the edge of the nest. The young dried off quickly. They are covered with a moderate amount of white, dark brown, and almost black down. The down faded slightly before the young acquired feathers.

The first day of hatching most Louisiana Heron nests contained one young, but some nests held two or three. They averaged 2.2 chicks the first day (25 nests, range 1-3, S.D. = 0.86). The next day most nests held three, a few had two or four, and a very few still had one. They averaged 2.7 chicks on the second day (23 nests, range 1-4, S.D. = 0.86). On the third day most nests had three or four, a few still had two, and they averaged 3.1. The fourth day they averaged 3.1 young, and finally on the fifth day the fifth young hatched in some nests.

An average of 3.7 young hatched per nest (29 nests, range 2-5, S.D. = 0.78). Hatching took an average of 3.4 days per clutch (24 nests, range 2-5, S.D. = 1.11). Four was the most frequent number of young hatching, three was next most frequent, and a few broods contained five or two young. At least one young was lost from every nest in which five young hatched. Considering broods of all ages three was the modal number of young.

Louisiana Herons brooded continuously until the young were several days old. Since they bred early in the season they only occasionally needed to shade either the eggs or the hatchlings. There was little apparent change in adult behavior at hatching except that the birds seemed

to move around on the nest more. Both parents continued brooding. When the young were several days old, by which time the youngest was large enough to hold up its head, the adults left them alone while they both hunted for food. The adults continued to brood the chicks at night.

Until the young were a few days old they were unable to hold up their heads more than momentarily. During this period they spent most of their time resting. They fed by picking up food the adults regurgitated into the nest. After they became able to hold their heads up they were able to take food directly from the parent. By the time they were about two weeks old they could reach into the adult's gullet and seize the food on its way up.

Mortality of Eggs and Young

Although some eggs were lost before incubation started only a few eggs were lost during incubation. From laying until just before hatching egg mortality was only 3.9 per cent. The hatching mortality was 10.5 per cent, and the minimum mortality during laying, incubating, and hatching was 14.0 per cent.

The average number of hatchlings surviving until two days after the last one hatched was 3.4 per nest (30 nests, range 1-5, S.D. = 1.08), this is not significantly less than the number that hatched ("t" = 1.31). The number was further reduced to 3.1 by the seventh day after hatching (31 nests, range 1-5, S.D. = 0.85), which is not significantly less than the number alive at two days ("t" = 1.09). Two weeks after hatching an average of 2.8 young survived (31 nests, range 1-4, S.D. = 0.77), which is not significantly fewer than were alive at one week ("t" = 1.63). However, the number of young alive decreased significantly

between the second day after hatching and two weeks ("t" = 2.59). Some older young started leaving the nest when the youngest was about two weeks old and later estimates of losses were less reliable. One chick (0.94) was lost per nest (27 nests, range 0-3, S.D. = 0.71) during the first two weeks of nest life, a nestling mortality of 18.3 per cent. Most of this loss was due to the starvation of the youngest chick in many clutches. When the last chick hatched as late as five or more days after his oldest sibling he started nest life at a severe disadvantage. While the young were small and feeble the adults regurgitated food onto the floor of the nest from which the young picked it up. When two or three of the nestlings developed to the point where they went to the parent, reached down into its throat and took the food, the nestling only strong enough to pick food off the nest floor usually got none. Typically only one young starved in a nest (17 of 19 nests in which young starved) but in two nests two did; and in about one out of every three nests none starved.

Another peak in mortality occurred when the young left the nest and started climbing about in the bushes and trees. In spite of their agility and tenacity a few fell to the ground, but at Lake Alice where the vegetation was low and bushy most of those individuals got back into the nest trees. Occasionally one became hung in the trees. One I found dead in 1960 had fallen during a storm from the top of a particularly high nest and landed on its back in a narrow fork of a branch where it died. Bent (1926) also found young that had become entangled in the vegetation and died, but he also notes that the young climb and swim well.

FEEDING

A cursory comparison of the feeding behavior of the herons on Payne's Prairie and in other feeding areas around Gainesville indicates that these birds are all feeding essentially the same way; that is, they are wading around in shallow water catching and eating small animals. The notable exception is the Cattle Egret which regularly feeds in company with cattle on higher and usually drier ground. However, any comparative generalization on their foods must be based on an analysis of food habits.

When they become excited or are disturbed, young herons often regurgitate their last meal, which they cast up as a pellet. By systematically collecting these pellets it is possible to acquire a series of heron meals without collecting the birds. The technique has two distinct advantages. (1) Because a large series of pellets is potentially available, the collector can reject pellets which show advanced or even moderate digestion, and (2) especially with less common species, pellets can be repeatedly taken from the same individuals. When the heronry is full of flightless young it should be an ecologically significant time to study the food habits of the herons, because in order to feed themselves and their young the adults must gather substantially more food per day than at any other time of the year.

Food apparently is abundant in the Gainesville region during the time of year the adults were feeding young because at that time plant growth was rapid, temperatures were high, and water levels were up. In spite of a probably adequate supply of food, an average of nearly one young per nest starved to death in nests of three of the four heron species studied. The adults' need for food for themselves and their ravenous young exceeded their food catching ability. It seems reasonable to assume that the birds were operating near their maximal efficiency. If this is true the birds were probably catching the kind of food they could catch the most of and were searching for it in the places where it was most often available to them. Differences in feeding behavior and in food habits would probably be amplified during this period of stress while the adults are feeding young.

Feeding Behavior of Adults

The feeding behavior of the various herons was strikingly similar. In most of their feeding activities they employed certain basic techniques which are common to all species. Each species employed its own variations of these techniques and the frequencies with which each of the several techniques was used varied among the four species.

The Ardeidae are opportunistic birds, not only as a group, but also as individual species and as individuals. They take advantage of a wide variety of food sources and employ a variety of feeding patterns to catch food. They are quick to take advantage of an abnormal bounty, and groups composed of several species would gather around any temporary concentration of food. Although there are many interesting variations, practically all feeding behavior of adult herons around Gainesville falls

into three general, though not necessarily distinct categories: (1) Stand and Wait; (2) Wade or Walk Slowly; and (3) Active Pursuit. The first two categories (names from Meyerriecks, 1960) are specific types of feeding behavior and are typical of the herons. These two types show several modifications; but the more unusual and dramatic means of gathering food are mostly variations of Active Pursuit.

In the Stand and Wait type of feeding, the heron finds a likely place, poses his body in readiness, and remains motionless. The heron remains immobile and eventually makes a strike if food approaches; if not it moves to a new place. The body may be held low and horizontal with the ankles flexed and the neck slightly withdrawn in a soft "s" curve; or the body may be held upright, the feet and legs straight, and the neck extended. Herons will hold these positions for many minutes, but may sometimes change from one of them to the other.

The Walk or Wade Slowly type of feeding has many elements in common with the Stand and Wait type, and resembles a slow moving variant of Stand and Wait. Walk or Wade Slowly is the fundamental stealth technique and is an important part of the feeding repertoire of many herons. The body may be held horizontal with the neck slightly withdrawn and the bill pointed forward; or the body may be upright with the neck straight and the bill pointed downward at about a 45 degree angle. The body, neck and head are usually held rigid as the heron moves, but the neck sometimes bobs slightly with each step, or just before making a strike the head may be withdrawn slightly or it may be undulated sideways. As the bird moves, each foot is lifted, extended, and lowered quite deliberately; the body is simultaneously moved smoothly forward. The bird may "freeze" just before a strike. Birds

hunting by the Stand and Wait technique often feed in the Wade and Walk Slowly technique while they are moving from one stand to another.

Active Pursuit includes Meinertzhagen's (1949) type, Disturb and Chase; but the most frequent form of Active Pursuit in the Gainesville region is simply walking or running in shallow water, chasing fish and making strikes here and there. A frequent ploy of several species is to walk through fields, or along the edge of a pond, or any likely place catching insects, frogs, or fish that flush at the heron's approach. This differs from Wade or Walk Slowly in that the body is not held horizontal or rigidly, the neck is not necessarily held rigid but typically moves forward and backward with each step; in other words the bird is not "sneaking up" on anything, but only catching what it sees and this is most often something which is moving out of the heron's way. The birds use many other types of Active Pursuit, and these form the basis of the many notes published on "unusual" heron feeding behavior; but these more unusual feeding patterns are used only infrequently by the Lake Alice birds during the breeding season. Reaching down and taking food from the water while on the wing (Hovering of Meyerriecks, 1960) is one of the more frequent of these unusual types, and has been reported in the Gainesville area (Dickinson, 1947).

Snowy Egret

Adult Snowy Egrets employ the Stand and Wait techniques of feeding more than any other feeding method. They also commonly feed by use of the Wade or Walk Slowly technique, sometimes feeding thus in grasslands away from water. During the summers Snowy Egrets occasionally associated with cattle. They would walk along near a cow and catch prey disturbed

by it very much the way Cattle Egrets feed. While with cattle, Snowy Egret behavior appeared to be intermediate between merely walking along and flushing prey and Wade or Walk Slowly. Snowy Egrets, more often than any of the other herons, fed by some form of Active Pursuit. They would frequently dash about through very shallow water twisting, turning, stopping and taking off in new directions, striking here and there at the fish. Snowy Egrets would often interrupt more deliberate types of hunting to chase after fish in shallow water and sometimes would run along a fairly steep canal or stream bank.

Snowy Egrets are social feeders and many individuals would gather to feed in a small area where there was a local abundance of food. Groups of 5 to 25 or sometimes more, often congregated around culverts and along small streams following heavy rains and a rise in the water level.

Young Snowy Egrets readily regurgitated their last meal when disturbed. Nestlings only a few days old did not become as distressed as did one to two week old young when they were disturbed, and they did not usually regurgitate. If one sibling was much less developed than his nest mates, he often ate the food his older and more excitable siblings regurgitated into the nest. Snowy Egret pellets were compact and held together rather well. If the young had been fed recently, each typically produced two pellets when disturbed.

The contents of the 50 analyzed pellets were: fish 87.8 per cent by volume, invertebrates 7.1 per cent, and amphibians 4.8 per cent. Table 5 lists the prey taken, the total number found in all 50 pellets, and the per cent of the total volume of each prey item. A total of 46 amphibians were eaten and 35 of them were tadpoles. These were particularly small tadpoles and taken altogether they comprised only 2.9 per

Table 5.--Analysis of Fifty Pellets Regurgitated by Young Snowy Egrets

	Number of Individuals	Per Cent of Total Volume
INVERTEBRATES		
Oligochaeta	1	tr.
Astacidae	6	0.70
Palaemonetes spp.	7	0.28
Zygoptera	7	0.06
Anisoptera (5 nymph)	18	1.00
Locustidae	188	2.78
Tettigoniidae	99	1.47
Gryllidae	32	0.47
Hydrophilidae	15	0.17
Corixidae	4	0.04
Arachnida	1	0.04
VERTEBRATES		
unidentified tadpoles	19	1.21
Acris gryllus	10	1.06
unidentified Hylid tadpoles	14	1.28
unidentified Rana spp. tadpoles	2	0.43
Rana pipiens	1	0.85
Elassoma spp.	42	1.08
Enneacanthus gloriosus	2	1.49
Enneacanthus obesus	12	5.31
Esox americanus	15	8.29
Etheostoma barratti	21	1.06
Fundulus chrysotus	37	6.80
Gambusia affinis	456	36.14
Heterandria formosa	224	3.08
Jordanella floridae	195	20.83
Lepomis macrochirus	8	2.34
Leptolucania ommata	1	0.04
Lucania goodei	9	0.21
Micropterus salmoides	3	1.23

cent of the total diet. A few cricket frogs (10 Acris gryllus) and one leopard frog (Rana pipiens) were taken.

Grasshoppers and crickets (Locustidae, Tettigoniidae and Gryllidae combined, 4.8 per cent) were only about as important in the over-all diet as were the amphibians. Most of the pellets contained a few insects, and 2 of the 50 contained no fish but were composed entirely of insects and amphibians. Dragon-flies (Anisoptera) were also important invertebrate food; five nymphs and 13 adults being taken. A few crayfish and fresh-water shrimp (Astacidae and Palaemonetes spp.) were included, especially early in the season.

Mosquitofish (Gambusia affinis) was the most important as well as the most numerous prey taken. Flagfish (Jordanella floridae) was second most important. Each of the other prey species was much less important in the total diet than were these two. Redfin pickerel (Esox americanus) was third, the golden topminnow (Fundulus chrysotus) was fourth, and the banded sunfish (Enneacanthus obesus) was fifth in over-all importance. Six other species were less important, comprising from 1.1 to 3.1 per cent of the diet. One of these, the least killifish (Heterandria formosa) was the second most frequently taken prey species, 224 individuals were included in the 50 pellets.

The pellets averaged 29.0 individual prey items. They included an average of 0.9 amphibians, 7.6 invertebrates, and 20.5 fish. The most important prey species, mosquitofish, flagfish, redfin pickerel, golden topminnow, and banded sunfish, comprised 77.2 per cent of the total diet. Mosquitofish were included 456 times in the 50 pellets and the least killifish was the second most numerous prey with 224 individuals taken. In addition to the 50 pellets discussed above, at least 200 other pellets

were studied in the heronry, but were not collected, and another 24 pellets that were collected are not included in the analysis. These additional gross observations tend to verify the preceding observations.

According to Baynard (1912), 50 pellets regurgitated by young Snowy Egrets at Bird Island, Orange Lake, contained 120 small suckers, 762 grasshoppers, 91 cut-worms, 2 small lizards, 29 small crayfish, and 7 small moccasins. Because Snowy Egrets from Orange Lake feed in places similar to those where the Lake Alice birds feed, it is difficult to explain the differences in food. Baynard's taxonomic categories are too vague to allow careful comparisons.

Cattle Egret

During the breeding season Cattle Egrets fed in grasslands and open meadows, and although they occasionally fed in wet places, they mostly fed away from water. They fed by walking along near the head or side of a grazing cow and caught prey flushed by the cow. However, they would occasionally wander from cow to cow, or even less frequently they would take short excursions away from a cow, and at these times they caught food they disturbed themselves. Individual Cattle Egrets would occasionally feed by themselves, independent of large ungulates, but although frequently noted during the winter this method of feeding was relatively uncommon during the breeding season.

Cattle Egrets are social birds and nearly always fed in small groups. Early in the season they usually fed in groups of 5 to 25 individuals, but in the middle of the nesting season, when many of the adults were feeding young, they most often fed in small groups of up to five or six individuals.

Young Cattle Egrets readily regurgitated their last meal when they were disturbed, and they were more easily disturbed than were the other species. When one young started regurgitating, the other young in the tree immediately started regurgitating, and 25 or 30 pellets would quickly rain down out of a tree. The pellets appeared to be composed almost entirely of grasshoppers with an occasional small frog or snake. The pellets were very neatly packed and were held together by mucous. If they had been fed recently, most young Cattle Egrets would produce two pellets.

The 50 pellets studied were composed of invertebrates 63.2 per cent by volume, amphibians 32.3 per cent, and reptiles 4.4 per cent. The analysis of the 50 pellets on which this discussion is based is presented in Table 6. Reptiles are relatively unimportant, only three snakes are included in the 50 pellets.

Amphibians were an important part of the diet of young Cattle Egrets. The 50 pellet sample included 101 frogs and toads. The leopard frog was the most important amphibian volume-wise although it involved only 23 individuals as compared with 69 individuals of the volumetrically second ranked cricket frog. One eastern spadefoot (Scaphiopus holbrooki) was included. Eight other individual amphibians were recorded: four treefrogs (Hyla spp.), two narrow-mouthed toads (Microhyla carolinensis), and two unidentified frogs. Together these eight individuals contributed only 2.0 per cent to the total diet. These, as well as the spadefoot were probably accidental and incidental in the diet.

Short-horned grasshoppers (Locustidae) are the most important prey of Cattle Egrets. Locustids were found in 48 of the 50 pellets. The other two pellets were each composed of one large leopard frog. Crickets

(Gryllidae) were the second most important invertebrate prey, but contributed less volume to the diet than did leopard frogs. The third most important invertebrate, long-horned grasshoppers (Tettigoniidae) were less important than even the cricket frogs. Collectively, the orthopteran insects contributed 56.6 per cent of the diet by volume. Spiders (Arachnida) were taken regularly; 88 were included in this sample. The other invertebrate groups (Table 6) each contributed less than 1 per cent of the diet and appeared to be taken accidentally.

The pellets contained an average of 34.1 prey items: 0.1 snakes, 2.0 amphibians, and 32.0 invertebrates. The four most important prey groups, short-horned grasshoppers, leopard frogs, crickets, and cricket frogs, comprised 78.8 per cent of the total diet.

In addition to the 50 pellets discussed at length above, 50 more were collected, and about 500 more pellets were studied in the heronry, but not collected. For the most part these observations essentially verified what has been already said and only add a few species to the list of prey. The most unusual pellets found were a group of about eight pellets collected on June 23, 1960. They were composed entirely of 30 to 50 mm., terrestrial beetle larva (Coleoptera).

Except for occasional single-stomach analyses, there appear to be no previously reported quantitative reports on Cattle Egret food. Their diet is described as very varied, practically omnivorous (Mackworth-Praed and Grant, 1957). Other than this one report, the Cattle Egret is recognized as primarily being a grasshopper feeder. Grasshoppers are noted as being of first importance in India (Whistler, 1949), in South Africa (Skead, 1956), and throughout its range (Witherby et al., 1947).

Table 6.--Analysis of Fifty Pellets Regurgitated by Young Cattle Egrets

	Number of Individuals	Per Cent of Total Volume
INVERTEBRATES		
Zygoptera	1	0.01
Anisoptera	5	0.58
Locustidae	679	36.21
Tettigoniidae	279	6.85
Gryllidae	523	13.50
Coleoptera	10	0.17
Elateridae	1	0.01
Curculionidae	2	0.01
Diptera	3	0.12
Tabanidae	5	0.54
Lepidoptera	2	0.12
Arachnida	88	5.15
VERTEBRATES		
Scaphiopus holbrooki	1	1.25
unidentified frogs	2	0.83
unidentified Hylidae	2	0.42
Acris gryllus	69	13.29
Hyla spp.	2	0.42
Rana pipiens	23	15.78
Microhyla carolinensis	2	0.42
Thamnophis sauritus	1	2.08
Thamnophis sirtalis	1	1.66
Tantilla coronata	1	0.62

Most reports on its food habits describe the beneficial aspects of Cattle Egrets removing ticks from grazing animals, but Skead reports that in South Africa the Cattle Egret only rarely removes engorged, conspicuous ticks from cattle even when the ticks are abundant, and no ticks were found in Lake Alice pellets. Besides a wide variety of insects, Cattle Egrets eat arachnids (Solfuges et al.), centipedes, frogs, toads, clawed toads (Xenopus spp.), lizards, and mice. There is even one second-hand report of a Cattle Egret eating a bird (Zosterops spp.) in South Africa (Whistler, 1949, Skead, 1956, and Witherby et al., 1947).

Little Blue Heron

The principal feeding technique employed by Little Blue Herons was the Wade or Walk Slowly, but they also used the Stand and Wait technique. Little Blue Herons would frequently "freeze" while wading, they would slowly lower the head and neck, then strike. Although a few individuals fed far from water, especially late in the season, most Little Blue Herons fed in water a few inches deep around the edges of ponds and on the prairies. The Little Blue Heron did not feed in social groups as often as the Snowy and Cattle Egrets did, but several individuals often fed in the same general area.

Young Little Blue Herons readily regurgitated their last meal at the least disturbance. The very young sometimes dropped the pellet into the nest and later re-ate it. Older individuals, generally, spewed a rather neat pellet over the edge of the nest, or, later, from their perch on a limb. These pellets appeared to be composed of a wide variety of food stuffs. A conspicuous feature was the frequency with which relatively large prey items were eaten. A redfin pickerel of

12 cm. or more, or a bullfrog (Rana catesbeiana) with a snout-vent length of 6 to 8 cm. frequently composed the entire pellet.

The contents of the 50 Little Blue Heron pellets was: amphibians nearly 54 per cent by volume, fish 32.5 per cent, invertebrates 12 per cent, and reptiles nearly 1 per cent (see Table 7 for detailed analysis). Reptiles were represented by two snakes.

Crayfish and spiders were the only invertebrates that contributed substantially to the total food. Most of the spiders, dystiscsids, and orthopterans listed on the table were from 10 pellets collected on June 10 and 13. These mid-June pellets were also unique in other ways and are discussed later.

The golden topminnow was the most important fish prey; it comprised nearly as much volume as the other eight fish species combined. The very similar banded topminnow (Fundulus cingulatus) was second in importance, and the least killifish was third. Although the least killifish was slightly less important volumetrically, in the diet of the Little Blue Heron young than was the banded topminnow, it was noted 10 times more often than was the banded topminnow. The other six species of fish eaten each contributed from 1.0 to 2.6 per cent of the total volume of food.

Large ranid tadpoles (Rana spp.) and adult bullfrogs were the two most important prey in this sample of 50 pellets. Although the sample included 27 ranid tadpoles, the four bullfrogs nearly equalled them in volume and together they comprised 34.1 per cent of the diet. Leopard frogs were about half as important, and the green treefrog (Hyla cinerea) was fourth in importance. Small unidentified ranids and one pig frog (Rana grylio) were next in importance. Six newts (Diemictylus

Table 7.--Analysis of Fifty Pellets Regurgitated by Young Little Blue Herons

	Number of Individuals	Per Cent of Total Volume
INVERTEBRATES		
Hirudinea	1	0.02
Astacidae	6	5.13
Palaemonetes spp.	3	0.10
Anisoptera (5 nymph)	15	0.91
Locustidae	11	0.53
Tettigoniidae	8	0.30
Gryllidae	10	0.08
Gryllotalpidae	1	0.12
Ephemeridae	2	0.12
Coleoptera (larvae)	4	0.34
Dystiscsdae	12	0.55
Belostomatidae	4	0.10
Hydrophilidae	1	0.02
Tabanidae	1	0.02
Arachnida	73	3.96
VERTEBRATES		
Diemictylus viridescens	6	1.18
unidentified tadpoles	2	0.18
Acris gryllus	2	0.18
Hyla spp.	2	0.59
Hyla cinerea	6	4.73
unidentified Rana spp. tadpoles	27	17.15
Rana spp.	17	2.60
Rana catesbeiana	4	16.95
Rana grylio	1	2.37
Rana pipiens	7	7.88
Seminatrix pygaea	1	0.69
Thamnophis sirtalis	1	0.08
Chaenobryttus gulosus	2	2.60
Enneacanthus obesus	2	0.99
Esox americanus	3	2.37
Fundulus chrysotus	50	14.78
Fundulus cingulatus	10	4.53
Gambusia affinis	28	1.58
Heterandria formosa	105	3.15
Jordanella floridae	8	0.99
Micropterus salmoides	7	1.38

viridescens) were found in pellets from three different nests. Therefore, this supposedly noxious amphibian was of moderate but regular occurrence in the diet of young Little Blue Herons at Lake Alice.

The pellets averaged 8.9 prey items and were composed of an average of 3.0 invertebrates (including 1.5 spiders), 1.5 amphibians, less than 0.1 reptiles, and 4.3 fish. The most important prey in volume were: ranid tadpoles, bullfrogs, golden topminnows, leopard frogs, crayfish, green treefrogs, banded topminnows, and spiders, in that order. These eight forms comprised 75.1 per cent of the diet. Three items stood out as being of prime importance: tadpoles, bullfrogs, and golden topminnows.

Many additional pellets, at least 200, were studied in the heronry but were not collected or preserved. These pellets verified the material collected and added one very interesting observation. Late in the season, from mid-June through July, when few young Little Blue Herons remain in the heronry, there was a major shift in their food. Fish became much less important; tree frogs, spiders, and orthopterans became predominate. The general trend was away from aquatic and toward more terrestrial prey. Many adults fed in open grasslands and pastures during mid-summer. Little Blue Herons wading through the grass and "peering over" in their typical Wade or Walk Slowly technique were as frequently seen as those wading in water.

Baynard (1912) analyzed the contents of 50 pellets regurgitated by young Little Blue Herons at Orange Lake. They contained 1,900 grasshoppers, 37 small frogs, 149 cutworms, 8 lizards, and 142 small crayfish.

E. A. Chapin analyzed 46 Little Blue Heron stomachs (Howell, 1932) and although the source of the birds was not stated the stomachs

were probably from several localities and probably collected throughout the year. Crustaceans (principally crayfishes) composed 45 per cent of the total food, small fishes (mainly minnows and killifishes with a few catfishes and sunfishes) composed 27 per cent, insects composed 16.5 per cent and frogs, small snakes, and turtles made up 8.5 per cent.

Meanley (1955) analyzed 50 Little Blue Heron pellets which he collected in Arkansas. He presented his data as frequency of occurrence. A wide variety of insects, primarily aquatic forms, were eaten. Frogs, especially leopard frogs, appear to have been quite important (found in 14 of 50 pellets). Crayfish were very important (12 pellets). Fish appear to have been less important, only a few species were taken: Lepomis spp. (7 pellets), Esox spp. (2 pellets), and undetermined fish (6 pellets).

Louisiana Heron

During the breeding season Louisiana Herons usually fed by stealth, both the Stand and Wait, and Wade or Walk Slowly techniques being used. In addition to feeding in ponds and on the prairies, Louisiana Herons were often seen standing immobile along the edges of canals and ditches. When wading they often held the body parallel to the water, and the head slightly retracted, and the neck shortened in an "s" curve. They typically waded in deep water and often waded in water so deep that it came up to their thighs, and sometimes to the belly.

The Louisiana Herons occasionally feed by employing some form of the disturb and chase technique. A Louisiana Heron would run through shallow water herding fish toward shore and trying to prevent their escape to deep water by waving its wings. It sometimes hovered or flew low across

open water and reached down into the water with the bill to grab something as it flew by.

In the Gainesville area the Louisiana Heron is a solitary feeder. Feeding individuals were widely scattered across the prairies and many of them fed along streams and in ponds away from the prairie.

Young Louisiana Herons regurgitated their last meal much less readily than did young of the other species at Lake Alice. When disturbed, the older young readily moved out of the nest and climbed up into the tree, but they often failed to regurgitate. Sometimes they could be forced to regurgitate by shaking their tree, yelling, banging on the limb and generally annoying them for 5 or 10 minutes, but most of the time this too failed. When they did regurgitate they did not usually produce a neat pellet, but typically scattered individual fish about the ground beneath the tree. It was often impossible to collect more than a few pellets from a brood throughout its whole nest life.

The 50 pellets were composed of fish, 95.4 per cent by volume, various invertebrates, 4.2 per cent, and amphibians, 0.2 per cent (see Table 8 for a detailed analysis). Only one frog, a cricket frog was included in the 50 pellets. This one record shows how unimportant amphibians were in the diet of young Louisiana Herons, and frogs are here regarded as accidental.

The only invertebrates of importance in the over-all diet were odonates. Of 58 invertebrates eaten 28 were dragon-flies and 8 were damsel-flies (Zygoptera). Together they represented 3.2 per cent of the total diet. One of the dragon-flies was a nymph and the other 27 were adults. Because of their long membranous wings these insects were

Table 8.--Analysis of Fifty Pellets Regurgitated by Young Louisiana Herons

	Number of Individuals	Per Cent of Total Volume
ARTHROPODA		
Palaemonetes spp.	2	0.23
Zygoptera	8	0.25
Anisoptera (nymph)	28	2.92
Tettigoniidae	4	0.20
Gryllidae	9	0.17
Belostomatidae	2	0.20
Hydrophilidae	1	0.03
Dystiscsdae	2	0.08
Diptera	1	0.03
Arachnida	1	0.08
VERTEBRATES		
Acris gryllus	1	0.17
Chaenobryttus gulosus	9	1.27
Elassoma spp.	30	0.79
Enneacanthus gloriosus	1	0.57
Enneacanthus obesus	1	0.42
Fundulus chrysotus	81	22.37
Fundulus cingulatus	19	7.93
Fundulus notti	8	1.13
Gambusia affinis	205	13.88
Heterandria formosa	143	4.53
Jordanellae floridae	210	36.82
Leptolucania ommata	1	0.08
Lucania goodei	4	0.11
Micropterus salmoides	5	1.98
Molliensa latipinna	11	2.83
Pomoxis nigromaculatus	4	0.91

conspicuous in the pellets. Their occurrence was sufficiently frequent to preclude the assumption that they are taken rarely or by accident, as is assumed for the other invertebrates. It would be interesting to learn whether they were taken opportunistically or whether the birds made a concerted effort to catch them. Their inclusion in the regular diet may be of further significance in understanding the Louisiana Heron's total ecology. The other 22 invertebrates showed wide variety and altogether comprised 1.0 per cent of the food.

The flagfish was by far the most important prey species taken. More individual flagfish, 210, were taken than any other species. Golden topminnows were extremely important in the diet although only 81 of them were included as opposed to 205 individuals of third in importance mosquitofish. The banded topminnow was fourth in importance, and the least killifish was a relatively poor fifth in importance although a total of 143 individuals were taken. Sailfin mollies (Molliensa latipinna), fingerling largemouth bass (Micropterus salmoides), warmouth (Chaenobryttus gulosus), and starhead topminnows (Fundulus notti) composed from 2.8 to 1.1 per cent of the diet and were next in importance. The remaining seven fish species each contributed less than 1 per cent to the diet and involved from one to four individuals each except for 30 individual pygmy sunfish (Elassoma spp.).

The pellets averaged 15.8 food items: amphibians less than 0.1, invertebrates 1.1, and fish 14.6 individuals. The three most important prey species, flagfish, golden topminnow, and mosquitofish, comprised 73.1 per cent of the diet.

Young Louisiana Herons regurgitated so infrequently that probably no more than another 50 pellets were seen but not collected in the heronry. These observations generally substantiate what is written above, and none of these other pellets contained frogs.

Baynard (1912) analyzed 50 pellets regurgitated by young Louisiana Herons at Orange Lake and found 2,876 grasshoppers, 8 small frogs, 17 cutworms, 6 lizards, and 67 small crawfish. These results are inconsistent with my finding at Lake Alice and cannot be explained. The findings of E. A. Chapin (Howell, 1932) who analyzed 48 Louisiana Heron stomachs, were more consistent with my data. Although not stated the stomachs he analyzed were probably collected at all seasons throughout their range: killifish composed 68 per cent of the total food in these stomachs, crustaceans (mainly prawns and a few crawfish) composed 20 per cent, and the balance included clam worms, spiders, weevils, grasshoppers, giant water bugs, dragon flies, water beetles, and ground beetles.

COMPARISON OF REPRODUCTIVE HABITS OF THE SPECIES

The breeding histories of Snowy Egrets, Cattle Egrets, Little Blue Herons, and Louisiana Herons are quite similar, but there are differences in the details and these vary from the most trivial to some of real ecological significance. Some of these differences amongst species are the direct result of their interspecific relationships within the heronry during the breeding season, and others are the result of differences in the total biology of the species. Unfortunately there are practically no qualitative studies on any phase of the biology of these birds with which the data from Lake Alice can be related. In this chapter, the breeding of each of the four most abundant species at Lake Alice will be compared.

Nest Site

In 1958, the various species of herons appeared to be selecting slightly different nest sites. The result of these differences was a vertical stratification of the nests. In 1958, Snowy Egrets nested at lower and more exposed sites than did the other species. Most of their nests were between three and five feet above the heronry floor, with a few up to a maximum of about ten feet. The birds built their nests around the edge of the heronry and around openings in the vegetation throughout the middle of the heronry. Little Blue Herons built their nests higher than did Snowy Egrets, mostly around ten feet and occasionally

still higher. Little Blue Heron nests were always built in better sheltered, sturdier appearing locations than were the Snowy Egret nests. Many Little Blue Heron nests were built against the main trunk of the nest tree. The Louisiana Heron nested at heights of 2 to 5 feet, much lower than any of the other species, but in contrast to the Snowy Egret, the Louisiana Heron nests were always in well sheltered places. Cattle Egrets started nesting in the middle of the heronry in the denser vegetation of the larger maples. Their nests were usually from 4 to 8 feet above the heronry floor in a variety of sites. Later in the season as the heronry spread, Cattle Egrets started nesting around the edge and openings of the new heronry as well as in the middle. It appeared that Cattle Egrets were selecting about the same type of nest sites as the Snowy Egrets did earlier in the season and that they differed from the Snowy Egret sites only in being slightly higher. The net result of this stratification was a reduction of interspecific competition.

In 1959, there did not appear to be any really systematic stratification of nests at Lake Alice. Most Louisiana Herons nested low in the bushes and some Cattle Egrets appeared to nest higher than did any of the other species. For the most part there appeared to be so much overlap, so many birds nesting from four to six feet above the heronry floor, that there was little effective separation of the species.

In 1960, more detailed observations were made. The heights of all nests in the study area and the species of all nest trees or bushes were recorded. The heights of the nests revealed some interesting features. Snowy Egrets and Louisiana Heron nests were consistently the lowest; nests of both these species averaged 5.7 feet above the water or ground.

Cattle Egrets nested substantially higher and their nests averaged 7.8 feet above the heronry floor. The Little Blue Herons nested at an average height of 7.2 feet throughout the season. The difference in nest height between Cattle Egrets and Little Blue Herons was significant ("t" = 2.08). As pointed out earlier there was a substantial difference in clutch size between early and late nesting Little Blue Herons. The Little Blue Herons that completed egg-laying by April 28 built their nests at an average height of 6.7 feet, but those that completed their clutches after April 28 nested at an average height of 8.5 feet. There was an obvious trend for the earliest breeding herons, regardless of species, to establish territories which included the lowest nest sites. These low sites tend to be sturdier than the high sites. The situation was somewhat confused by Little Blue Herons, because even the early nesting pairs selected slightly higher sites than did the contemporaneous Snowy Egrets and Louisiana Herons. However, the primary factor causing the stratification appears to have been the differences in the time of nesting. The general trend being for the earliest nesting pairs to build their nests in the lowest, and probably sturdiest sites available and for later nesting individuals to build their nests higher.

In 1960, the heron nests at Lake Alice were built only in shrubs or trees. The birds built their nests in red maple, buttonbush, elder, myrtle, or willow. Red maple was the most important nest site; 37.5 per cent of all heron nests were placed in red maple. Buttonbush was very important and held 28.4 per cent of all nests. Elder with 19.8 per cent of the nests is third in importance. Myrtle and willow with

8.2 and 6.0 per cent are considerably less important to the heronry as a whole.

A summary of the herons' nesting substrate is presented in Table 9. It is interesting that red maple is the most frequent nest site of all species except the Louisiana Heron. Buttonbush is the second most frequent choice of all the species. Louisiana Herons use elder more frequently than they use any other bush or tree and they use it much more frequently than do the other herons. The two tree species most frequently used for nesting by each heron species hold about two-thirds of the nests of that species, except for the Little Blue Heron. The Little Blue Heron shows stronger nest site preference than do the three other herons and builds 85 per cent of its nests in maple and buttonbush.

The four heron species do show differences in their nest site. There are three average nest heights: 5.7, 7.2, or less, and 7.8 feet. These effectively divided the four species into three groups. The two species that nest at lower elevations use different trees for nesting. One of them, the Louisiana Heron, uses elder most frequently and buttonbush next most often and builds many nests in myrtle. The other, the Snowy Egret, uses maple, buttonbush, and elder in that order, and only occasionally builds in myrtle and willow. Thus, although they both nest rather early, these species tend to have reduced interspecific competition because of the differences in nesting substrate. The Little Blue Heron builds its nests higher than these two species do, and the Cattle Egret builds its nest the highest of any of the herons.

Table 9.--The Species of Trees and Bushes Used by Four Species of Herons For Nest Building at Lake Alice, 1960

	Per Cent of Nests in Each Type of Tree				
	Maple	Buttonbush	Elder	Myrtle	Willow
Snowy Egret	43	26	18	6	7
Cattle Egret	33	29	19	12	7
Little Blue Heron	49	36	11	--	4
Louisiana Heron	11	29	39	18	7

Nest Building

In all four species the females build the nest with twigs and sticks that are brought to them singly by the males. Male Little Blue Herons and Cattle Egrets gather their twigs from bushes and trees near the nest site. The Little Blue Heron tends to hunt for twigs at all levels in the bushes and trees while the Cattle Egret tends to limit its collecting to the upper and outer reaches of trees and bushes. In general the Cattle Egret gathers smaller twigs than do the other species. Male Snowy Egrets gather all their twigs from the ground or from the water beneath the heronry. Some Snowy Egret nests, especially early ones, are built entirely of sticks that have lain beneath the heronry for a year or more and are weathered smooth and often covered with mud. But females of all species frequently drop twigs which they are attempting to work into the nest, and incomplete nests especially, and a few complete ones too, may be dismantled and the twigs scattered on the heronry floor. These twigs, including ones broken off by male Little Blue Herons and Cattle Egrets, are found and picked up by the male Snowy Egrets. The Louisiana Heron picks up twigs from the heronry floor in the manner of the Snowy Egret, but it also breaks twigs off low bushes and large fallen limbs. In all species there is a brief twig passing ceremony which generally involves elevating certain feathers, especially those of the crown. All species but the Cattle Egret spend an average of four to five days building the nest before the first egg is laid, at which time the nest is typically incomplete. The nest is completed during the egg laying period. Cattle Egrets spend an average of between six and seven days building the nest before they lay their first egg, or an average of about two days longer than the other herons. Most Cattle

Table 10.--Nesting Statistics of Four Species of Herons at Lake Alice

	Snowy Egret	Louisiana Heron	Little Blue Heron	Cattle Egret
Days to build nest	4.2	(4 or 5)	4.6	6.6
Days between laying	1.9	1.7	1.7	2.0
Number eggs laid	4.1	4.3	3.8	3.5
Number eggs in clutch	3.9	4.1	3.7	3.5
Incubation period (days)	22.4	23.8	22.8	22.9
Number eggs day before hatching	3.8	4.1	3.7	3.5
Number hatching	3.3	3.7	3.2	3.1

Egret nests are complete when the first egg is laid or are at least more nearly complete than are nests of the other species.

Egg Laying and Clutch Size

Most eggs were laid at two-day intervals, that is, the eggs were laid on alternate days. There were no intervals of more than two days. All Cattle Egret eggs were laid at two-day intervals. But occasionally Snowy Egrets, and even more frequently, Little Blue Herons and Louisiana Herons (see Table 10) laid eggs on consecutive days. Typically there was never more than one one-day interval per nest; exceptions tended to be limited to larger clutches.

Snowy Egrets, Louisiana Herons, and Little Blue Herons lost an average of 0.2 of an egg per nest between laying and completion of the clutch. Losses of eggs and their passage through the bottom of incomplete nests account for most of this loss. However, Cattle Egrets lost no eggs between laying and completion of the clutch. In spite of these early losses by the other species, the Cattle Egret still had the smallest clutch, and the differences in clutch size were sufficiently great that there must obviously be other differences in the life histories of these species.

Although their clutches were the smallest, Cattle Egrets did not have significantly smaller clutches than Little Blue Herons ("t" = 1.18). Neither did Snowy Egrets have significantly smaller clutches than Louisiana Herons ("t" = 1.65). All other differences in clutch size were significant, for example, the differences between Little Blue Heron and Snowy Egret clutches had a "t" of 3.46.

Although no intentional experiments were performed, the daily removal of eggs from some nests by predators and other egg losses lead to the conclusion that all four of these herons are indeterminate layers, but that the maximal number of eggs they can lay serially is about double the average clutch size for the species.

Incubation

The incubation periods of these herons are quite similar (see Table 10). The Snowy Egret has the shortest average incubation period, the Little Blue Heron and Cattle Egret require an average of about half a day longer. The Louisiana Heron requires one and a half more days for incubation than did the Snowy Egret, and a day more than do the two species with the intermediate incubation period. Because Louisiana Herons have the largest clutches, nest first when temperatures are still low, and do less late nesting than the other species, it could be reasoned that their longer incubation period is a result of the birds' inability to keep more eggs during cooler weather as warm as the other species do less eggs in warmer weather. However, there is no evidence to substantiate these ideas and no correlations between early and late, or small and large clutches could be made.

In all four species both sexes incubate. The adults stand over the eggs and shade them during mid-day in late spring and summer. Cattle Egrets shade their eggs more than the other species and in this case the difference is doubtless related to the later nesting of the Cattle Egrets.

Hatching and the Young

Young herons of all four species often call inside the egg before they pip. The eggs are usually pipped one day or slightly less, rarely two days, before the young emerge. The adults (of all species) remove the empty shells after each young hatches, and drop the shells over the edge of the nests. About the time the first egg is pipped the adults also remove any cracked or empty eggs even though they may have incubated them for the full period.

On the first day of hatching Louisiana Heron broods average 2.2 young; most of their broods are complete by the third or fourth day of hatching. Snowy Egret and Little Blue Heron broods average 1.5 and 1.6 young respectively on the first day of hatching, and most of their broods are complete by the third or fourth day of hatching. Cattle Egret broods average 1.1 young on the first day of hatching and most of their broods are not complete until the fifth day of hatching.

The average number of young hatching per nest is closely related to the number of eggs per clutch (see Table 10). Most Snowy Egret, Little Blue Heron, and Louisiana Heron hatchlings are brooded almost continuously during their first few days of nest life, but when they are able to hold their heads upright and strike at objects, the two parents simultaneously vacate the nest. Cattle Egrets spend considerable time shading the young, but individual young Cattle Egrets probably do not receive as much parental brooding and shading as do nestlings of the other herons. Cattle Egrets hatch over such a long period of time that both parents are off gathering food for the older nestling while the youngest are still so undeveloped that they would be continually attended if they were by themselves. The newly hatched young probably passively

receive many of the benefits of brooding from their older siblings. Also, since Cattle Egrets nest substantially later than the other species do, there is considerably less danger that the young might become chilled during the day.

The young dry off shortly after hatching. They are relatively helpless and remain in the nest for some time and have down growing only on the future pterylae. At first they are extremely weak and seldom peep or raise their heads but after two or three days they peep more and hold up their heads for relatively long periods. Although at first they pick food up from the nest floor they soon take it directly from the parent's bill and shortly reach down into the parent's gullet for the food.

There is no evidence that any of these birds raise two broods in one season although the over-all breeding season is sufficiently long for this to be done.

Mortality of Eggs and Young

Even before the first egg is laid various factors which increase mortality begin to operate. Wind often blows down nests that are just being started, in most cases this is probably due at least in part to the adults trying to build the nest at an impossible site. Other herons may try removing twigs from a temporarily unprotected nest, and if the nest is just started it usually falls to the ground. Even sturdy nests can seldom survive the removal of more than two or three twigs. These delays in nest completion often result in the bird's laying the first egg before the nest is complete enough to hold the egg.

The Cattle Egret spends considerably more time building its nests than do the other herons, and its nests are much more complete before they start laying. The Cattle Egret loses practically no eggs between laying and incubation while the other species lose between 3.9 and 5.4 per cent of their eggs (see Table 11). Not only are Cattle Egret nests more complete but the adults are more attentive, and incubation starts with the laying of the second egg.

Sometimes the birds never succeed in their efforts to build a nest. One nest that never reached completion was started on April 20, 1960; it was there the 21st, but completely gone the next day; on April 26 a nest was started at the same place, the next day it was a large nest, but a day later only a few twigs remained, and on April 30 there was no evidence of the nest; on May 3 it was started, but on May 5 it was gone; on May 7 it was started again, and on May 9 it was gone again. In 19 days this nest was started four times, and each time it lasted for at least two days, and it disappeared four times. This particular nesting effort was the work of a pair of Little Blue Herons. There was no activity at the site for the next month and a half, but in late June a pair of Cattle Egrets built a nest at the same site. They laid and hatched five eggs with no apparent difficulty.

Grackles or other predators may find a heron's nest and remove the eggs as regularly as they are laid. One Snowy Egret nest that was regularly robbed never did produce young. This particular nest was started on April 5, 1960. The first egg was found on the 11th and on the 13th there were two eggs. On the 14th there was only one egg, a new one, and the next day there were none; on April 17th the fourth egg was laid, and the next day it was gone and the nest again empty; on April 19

one egg was added, but it was removed by the next day. Then the clutch was completed; eggs being laid on the 21st, 23rd, and 5th of April, and incubation proceeded for nine days. On the 5th of June egg number two disappeared. On the 7th number one was gone, and on the 8th number three was gone. On the 9th the nest was reduced to a few twigs scattered beneath the tree. Most of these eggshells were recovered. They had been opened and eaten by birds, apparently Boat-tailed Grackles (Cassidix mexicanus).

Purple Gallinules (Porphyrula martinica) also take eggs from nests. Young Purple Gallinules feed on eggs brought to them by the adult birds. A few eggs that had been crushed inwardly until the outer shell was a cluster of tiny fragments held together by the membrane were found at widely scattered locations. They had apparently been taken and eaten by Rat Snakes (Elaphe obsoleta), the only arboreal snake seen in the heronry.

Fish crows (Corvus ossifragus) are common on the University campus adjoining Lake Alice. They often perched in trees around the lake, and nearly every day of the 1960 breeding season they were seen flying over the heronry. It is interesting that these fish crows were never seen in the heronry proper, and there was no mortality either of eggs or young that could be attributed to these birds. There was no evidence of any mamalian predation. In fact there was never any evidence of mammals other than mice having been in the heronry. Raccoons (Procyon lotor) and other potential mamalian predators are doubtless incompatible with the American alligator (Alligator mississipiensis) which is numerous at Lake Alice.

Alligators from one foot to six feet long and occasionally larger individuals scavenge in the heronry. These animals promptly eat dead nestlings, regurgitated fish and frogs and anything else remotely edible that falls to the heronry floor. In performing this scavenger service they keep the heronry largely free of the biological wastes that would have attracted Fish Crows, raccoons, or other potential predators.

A great many nests are blown down, destroyed, robbed, or deserted during construction, egg-laying and early incubation. Probably well in excess of half of the nests started never reach the point of containing a full clutch. Once the clutch is complete and incubation gets under way, the eggs are relatively safe. But even then predators manage to get a few nests, and when they do they generally take all the eggs, often removing them one at a time over a period of several days.

From the day before hatching starts through hatching there is a mortality of from 10 to 15 per cent (see Table 11). There is some loss of young to predators at this time. The adults are restless and they accidentally crush an occasional egg or young while moving around on the nest. Unaccountably the Snowy Egret nests suffered the highest hatching mortality. The over-all mortality from egg laying through hatching ranged from a low of 12.6 per cent for the Cattle Egret through a high of 19.3 per cent for the Snowy Egret. The Cattle Egret, Little Blue Heron, and Louisiana Heron had similar mortalities at hatching but the Cattle Egret's lack of loss in the egg laying period did much to suppress its over-all mortality.

Cattle Egrets lose practically no nestlings during the first two weeks after hatching. The Cattle Egret mortality of 5.7 per cent of its nestlings represents a loss of about one young from every five nests.

Snowy Egrets, Little Blue Herons and Louisiana Herons have a nestling mortality of from 25.4 to 32.6 per cent during the first two weeks. Most of this loss is due to starvation. The last sibling to hatch in practically all the larger clutches of these three species is usually so far behind his older siblings that he seldom gets enough food to survive for more than a few days. Only occasionally did more than one young starve in a nest. This loss averages about one young per nest, however young were seldom starved in broods as small as two. The Snowy Egret had the highest nestling mortality, while the Little Blue Heron and Louisiana Heron had very similar mortalities.

The over-all mortality of eggs and young from nests in which young eventually hatch varies from a remarkably low 17.5 per cent for the Cattle Egret to a surprisingly high 45.6 per cent for just the period from egg laying through the first two weeks of nest life (Table 11).

There is another period of rather high mortality when the young first leave the nest and start climbing about in the trees. Young often fall to the ground. At Lake Alice the vegetation is sufficiently bushy for these young usually to climb back to their nests, but at other places where herons nest in large mature trees, the inability of young that fall from nests to get back into the trees is an important factor in mortality. At Lake Alice a few young are caught by alligators before they get back in their tree, and Sprunt and Chamberlain (1949) report recovering bands from young Louisiana and Little Blue Herons from an alligator stomach. Strong winds and heavy rains result in losses; young are knocked from trees and are hung in vegetation or have their feathers matted with mud and pounded into the mud.

Table 11.--Mortality of Eggs and Nestlings of Four Herons, Lake Alice, 1960

	Mortality in Per Cent			
	Snowy Egret	Cattle Egret	Little Blue Heron	Louisiana Heron
Laying to day before hatching	5.4	0.0	3.9	3.9
Day before through hatching	14.7	12.6	12.1	10.5
Laying through hatching	19.3	12.6	15.6	14.0
Hatching through two weeks	32.6	5.7	26.2	25.4
Over-all mortality from laying through two weeks	45.6	17.5	37.6	35.8

Cattle Egret broods averaged 2.9 at the end of two weeks of nest life. Louisiana Herons averaged 2.8 young, Snowy Egrets averaged 2.6, and Little Blue Herons averaged 2.4. Although these Cattle Egret broods were not significantly larger than Louisiana Heron broods ("t" = 0.97), the Louisiana Heron clutches contained significantly more eggs than Cattle Egret clutches ("t" = 4.29). The Cattle Egret has such a low nesting mortality that in spite of its laying fewer eggs than the three other herons, it produces more young.

COMPARISON OF THE FEEDING HABITS OF THE SPECIES

The eating of different foods, or at least gathering their food from different areas would be the final proof that two or more herons are occupying different niches, that their ecologies are different.

Feeding Behavior of Adults

One occasionally finds dense little groups of Snowy Egrets and Little Blue Herons, and sometimes Louisiana Herons, clustered around a roadside culvert, along a small meadow canal, or on a pond. But it is unusual to find these three species gathered together and feeding on the same thing. Indeed, it is not usual to find concentrations of individuals of the same species gathered together in tight groups and feeding on the same prey. I once saw a group of about eight Louisiana herons and twice that many Snowy Egrets feeding together near Cedar Key. These birds were running around chasing fish and making strikes in all directions in a small pond, about 50 feet long by 10 feet wide, in which an unusually low tide had concentrated fish from an area of several acres. All examples of compact mixed feedings are not so clearly brought about by such an unusual and abundant supply of food, but they are usually related to sudden filling of areas, or their rapid drying. Such concentrations do not occur frequently but they do occur and their prompt use certainly reflects the adaptiveness of the herons.

In their day to day feeding the four herons seem to feed consistently in slightly different habitats. They are of course usually limited to areas where the water is not too deep (less than eight inches) and to areas where there is not too much vegetation. However, adult herons sometimes feed by flying low over the water, or hovering, and reaching down into the water to grasp prey in the bill, and they sometimes feed from floating objects. When they feed in these ways they are not restricted by depth; but these are not typical feeding techniques and are probably employed by the birds to enable them to take advantage of some unusual bounty. Snowy Egrets spend most of their time feeding in water a few inches deep, as do Little Blue Herons. Louisiana Herons feed in deeper water, and only rarely do Cattle Egrets feed in the water. In spite of the great amount of overlap and the similarity of the adults' behavior, there still appear to be significant differences.

Little Blue Herons often feed in somewhat more heavily vegetated areas, in more marsh-like places than do Snowy Egrets, which do much feeding in open areas of shallow water, although they too are often seen standing at the open water edge of emergent vegetation around ponds or small lakes. Snowy Egrets indulge more in Active Pursuit, running around in shallow water striking at fish, while the Little Blue Heron is more of a Stand and Wait, and Wade or Walk Slowly feeder. These differences might in part be due to differences in the types of areas in which they hunt. Active Pursuit, while successful in shallow, open water would be considerably less effective in deeper water or in denser vegetation.

The Louisiana Heron typically feeds in deeper water than does the Snowy Egret or Little Blue Heron. It often wades in water to a depth of its belly or leg feathers. The Louisiana Herons also feed along the edges of canals or other banks where the water drops off rapidly, and from floating or submerged vegetation in deeper water. Although in the Gainesville area it feeds primarily by stealth, it sometimes chases fish about in shallow water and takes prey from deep water by "hovering."

During the breeding season the Cattle Egret feeds almost exclusively in company with large animals, usually cattle. Its most important feeding areas are around the edge of Payne's Prairie and in the neighboring pasture lands. The Cattle Egret walks along beside the head or flank of a grazing cow and catches prey the cow flushes. Although cows frequently wander into the water, the Cattle Egret does most of its feeding in drier pastures and quickly abandons the cows if they wander into water deeper than two or three inches. Snowy Egrets sometimes associate with cows around Gainesville, but this is rather unusual behavior for them. However, Snowy Egrets and Little Blue Herons occasionally feed away from water and sometimes feed in high pastures quite far from water. In these places they feed by walking slowly through the grass catching prey that flushes at their approach, or, especially the Little Blue Heron, by the more stealthy Wade or Walk Slowly technique. I have not seen Louisiana Herons feeding in these areas.

Although observations of feeding adults do reveal differences between the species, these differences are neither sufficiently conspicuous, nor sufficiently great to be regarded as any more than

indicative that the birds, exclusive of the Cattle Egret, are doing different things.

Food Habits of the Young

The food of the young of the four herons, as determined by the analysis of 50 regurgitated pellets from each species is grouped into major categories and presented in Table 12. There are some conspicuous differences between species: the Little Blue Heron eats mostly amphibians, the Louisiana Heron and the Snowy Egret eat mostly fish, and the Cattle Egret eats primarily invertebrates. Differences in the degree of diversification of food are also conspicuous: the Little Blue Heron has a widely diversified diet and eats fairly large quantities of fish and invertebrates in addition to the amphibians. The Louisiana Heron and Snowy Egret have much less varied diets and practically limit themselves to fish. However, the Cattle Egret eats mostly orthopteran insects but does eat a great many amphibians and a few reptiles in addition to the invertebrates.

Snowy Egrets eat primarily fish and their pellets average 20.50 fish. The mosquitofish is the most important species with an average frequency of 9.0 per pellet and the least killifish is the second most frequently taken and averages 4.5 per pellet. The redfin pickerel was taken five times more often by Snowy Egrets than by Little Blue Herons and was not recorded from the Louisiana Heron. Mosquitofish and least killifish occur in most any water offering them shelter, but they are most commonly found in very shallow water, and the redfin pickerel is practically limited to such shallow water. The high frequency and importance of these three fish in the Snowy Egret diet and the frequency

Table 12.--Analysis of Contents of 50 Pellets Regurgitated By the Young of Each of Four Species

	Snowy Egret	Cattle Egret	Little Blue Heron	Louisiana Heron
	Per Cent of Total Volume			
Invertebrates	7.0	63.2	12.3	4.1
Fish	88.1	0.0	32.7	95.9
Amphibians	4.8	32.4	54.1	0.2
Reptiles	0.0	4.4	0.9	0.0
	Average Number of Items Per Pellet			
Invertebrates	7.56	31.96	3.04	1.11
Fish	20.50	---	4.30	14.64
Amphibians	0.92	2.02	1.48	0.02
Reptiles	---	0.06	0.04	---
All prey items	28.98	34.14	8.86	15.80

of very small tadpoles indicates that most of their food is taken in shallow water. The occasional appearance of sunfish or grasshoppers indicates that the birds occasionally feed in deeper or in drier areas.

Cattle Egret pellets include an average of 32 insects. The average number of individual prey items is 13.6 short-horned grasshoppers per pellet, 10.5 crickets, 5.6 long-horned grasshoppers, 1.8 spiders, 1.4 cricket frogs, and 0.5 leopard frogs. Young Cattle Egrets regurgitate no fish, tadpoles, aquatic invertebrates, or aquatic frogs. The food apparently all comes from upland situations, from open grasslands where meadow frogs are found, and these are the areas where the adult Cattle Egrets feed, though they do sometimes feed in wetlands and occasionally in water several inches deep. However, in addition to the 50 pellets reported on here, several hundred were checked in the field and 50 more from Lake Alice, and 50 more from each of three other localities were carefully analyzed and no purely aquatic prey with the questionable possibility of a few small beetles was found.

Though Little Blue Herons eat nearly three times as many fish as amphibians, the amphibians make up the largest bulk of their diet. They do not eat the same kinds of frogs that Cattle Egrets eat. While Cattle Egret pellets average 1.4 cricket frogs and 0.5 leopard frogs, Little Blue Heron pellets average less than 0.1 cricket frogs and only 0.1 leopard frogs per pellet. Little Blue Herons eat such aquatic amphibian forms as large ranid tadpoles and bullfrogs, 0.5 and 0.1 per pellet. Fish are important and golden topminnows, 1.0 per pellet, contribute by far the bulk of the volume attributed to fish. Banded topminnows, 0.2 per pellet, are the second most important fish. Relatively few

mosquitofish, 0.6 per pellet, are taken in comparison to the number of least killifish, 2.1 per pellet, and other fish taken. The ways in which the Little Blue Heron's fish diet differs from that of the Snowy Egret indicates that it feeds in deeper water than does the Snowy Egret.

Even compared to the highly piscivorous Snowy Egret, the Louisiana Heron stands out clearly as a fish specialist. The only important deviation from a straight fish diet is the inclusion of 0.6 dragon-flies per pellet. All four of these herons eat dragon-flies and the incidence of dragon-flies in the diet is greater when the incidence of fish is greater. The flagfish was both the most numerous, 4.1 per pellet, and most important, 36.8 per cent by volume, prey taken by Louisiana Herons. It is a shallow water fish but is found less frequently than are mosquitofish and least killifish in water from two inches to one-fourth inch deep. Flagfish are more readily found in water several inches deep. These last two species are the next most often taken fish, 4.1 and 2.9 per pellet, and the mosquitofish contributed only about a third as much to the over-all diet as did the flagfish. Although numbering only 1.6 per pellet, the second most important fish was the golden topminnow, another fish that probably ranges in deeper water than do mosquitofish and least killifish. Louisiana Herons also eat a few each of several other species of fish typically found in deeper water. The complete absence of tadpoles and near absence of frogs indicate that the adults do not usually feed in areas where they would be apt to find amphibians, that is, they probably do not normally feed in very shallow water or on temporarily flooded flats.

The flagfish makes up 36.8 per cent of the food of the Louisiana Heron, and the mosquitofish makes up 36.1 per cent of the Snowy Egret's food. The golden topminnow is second most important to the Louisiana Heron, but the flagfish is second most important to the Snowy Egret. The mosquitofish, first for the Snowy Egret, is third in importance to the Louisiana Heron, and the redfin pickerel, which is not recorded from Louisiana Heron pellets, is the Snowy Egret's third most important prey. There appears to be good basis here for considering these two strongly piscivorous birds to be fishing in different niches. The great number of mosquitofish and least killifish (456 and 224) and several redfin pickerel eaten by the Snowy Egret, argue for a very shallow feeding area. The reduced abundance of mosquitofish and least killifish (205 and 143) and increased abundance and importance of flagfish and golden topminnows in the Louisiana Heron diet indicates that this species feeds in deeper water. The inclusion of even a few warmouth, bluegill (Lepomis macrochirus), and black crappie (Pomoxis nigromaculatus) in the diet of the Louisiana Heron and their complete exclusion from the diet of the Snowy Egret also indicates that the Louisiana Heron is feeding in deeper water. Therefore the two fish-feeding birds can be regarded as utilizing mutually exclusive areas; one deep water and the other shallow.

The Little Blue Heron eats still different fish and although the fish it takes indicates that it feeds in deeper water than does the Snowy Egret, it eats practically no flagfish and therefore does not appear to be feeding in the same areas as the Louisiana Heron. The Little Blue eats a large number of topminnows which are extremely important in its diet.

These four herons show rather distinct differences in their feeding patterns: Snowy Egrets fish in shallow water, Louisiana Herons fish in deeper water, Little Blue Herons feed on amphibians and fish they catch in water of intermediate depths, and Cattle Egrets catch orthopteran insects and amphibians in relatively dry pastures.

The volume of the pellets regurgitated by the four herons shows considerable variation in spite of their apparent similarity in size. Little Blue Heron pellets average 10.15 ml., Louisiana Heron 7.06 ml., Snowy Egret 9.41 ml., and Cattle Egret 4.82 ml. There are at least four factors contributing to these differences: (1) there is a real difference in the size of the pellets, which is due in part at least to (2) the large size of some prey, for example, Little Blue Herons ate four bullfrogs which averaged 21.5 ml. Certain prey items (3) such as the few dragon-flies in Louisiana Heron pellets and the mainly intact insects in Cattle Egret pellets may occupy an excessive amount of space for their volume, and (4) small fragments and disarticulated insect appendages were excluded from the pellet analysis and as a result a substantial portion of every Cattle Egret pellet was discarded before its volume was measured.

The average number of food items per pellet varies markedly. Little Blue Heron pellets contain an average of 8.86 individuals, Louisiana Heron 15.80, Snowy Egret 28.98, and Cattle Egret 34.14. The number of prey items and the volume of the pellets were not correlated, but number of prey items and type of prey are correlated. Average size of the invertebrates eaten by Snowy Egrets and Cattle Egrets (0.09 and 0.10 ml.) is small because they consist mostly of Short- and Long-horned

grasshoppers and crickets. Little Blue Herons eat a few crayfish and the average invertebrate is five times larger (0.41 ml.). Little Blue Herons eat larger fish (average 0.78 ml.) than do either Louisiana Herons or Snowy Egrets (0.46 and 0.40 ml.), and this is due in part to the Little Blue Heron's eating several fish species of large size: topminnows, warmouth, banded sunfish, redfin pickerel, and others. The Louisiana Heron's and the Snowy Egret's fish prey include species of small size. Even the average size of fish of the same species eaten by these three birds differs. For example, the average volume of the golden topminnows is: Little Blue Heron, 1.50 ml.; Louisiana Heron, 0.98 ml.; and Snowy Egret, 0.86 ml., and the average size of the least killifish is Little Blue Heron 0.15 ml., Louisiana Heron 0.11, and Snowy Egret 0.07 ml.

Feeding Behavior as Related to Food

The food habits of these birds agrees closely with their feeding behavior. The Snowy Egret feeds mostly in shallow water and most of its food is fish, those species found most abundantly in shallow water. They occasionally feed in open grasslands away from water and sometimes feed with cattle, and a few of their pellets are composed entirely of grasshoppers and crickets. The Cattle Egret seldom feeds in wetlands except when a cow being used as a flusher or beater wanders into the water. The Cattle Egret feeds mostly in relatively dry pastures and seldom feeds independent of cattle. The Cattle Egrets eat mostly grasshoppers and crickets and although they eat many cricket frogs and leopard frogs, these two forms frequent grasslands and are not strictly

aquatic frogs. No aquatic forms are found in the food of Cattle Egrets. The Little Blue Heron is a strongly aquatic bird and although it occasionally feeds in pastures or around dried wood ponds, it mostly feeds in water a few inches deep, but not typically as deep as the Louisiana Heron feeds. Their pellets contain aquatic amphibians and fish. The Louisiana Heron is the most completely piscivorous of these birds, and the adults are never seen feeding away from the water. Louisiana Herons consistently feed in deeper water than do either Snowy Egrets or Little Blue Herons; here they catch only fish, primarily flagfish and an occasional dragon-fly.

CONCLUSIONS

In the course of this study information on the breeding and feeding biology of the Snowy Egret, Cattle Egret, Little Blue Heron, and Louisiana Heron was gathered. This information on breeding was presented and discussed in detail earlier in this paper. The comparative feeding behavior and food habits of the four herons were described and discussed also. With this information it is possible to make some tentative generalizations regarding the social relationships among the four herons and to augment what is known of their breeding ecology.

Nest Site

Although there is little contact among the four species of herons outside the breeding season, there is some contact among them during the breeding season. In establishing and defending their territories, males of all four species repel all herons of their own or of any other species that approach too closely. Herons establishing their territories later move in as close as possible to the holdings of the early arrivals. Males arriving late do not appear to select territories near males of their own species in preference to those of other species, but take up territories near those of any already-established individual, regardless of species. Social nesting in these herons thus tends to be with any heron species rather than species-restricted. In addition to this social nesting, the only evident relationships between these four

species are competitive in nature. The nesting habitats of these four herons at Lake Alice are slightly different. Snowy Egrets and Louisiana Herons nest early and at the same height, but for the most part they select different trees and bushes. The Louisiana Heron nests in elder and other bushes in open areas whereas the Snowy Egret nests in dense vegetation such as the maples which grow in the middle of the island. Little Blue Herons and Cattle Egrets nest in the same trees as do the Snowy Egrets, but they nest higher. These differences in nest heights result in a vertical stratification in the dense, tall vegetation with Cattle Egrets nesting above Little Blue Herons which in turn nest above the Snowy Egrets. There is also a horizontal stratification. The Louisiana Heron nests around the edge of the heronry and in other open areas. This complex stratification is not due to differences in the herons' preferences, and is therefore not always manifested.

In 1960, early Little Blue Heron nests averaged 6.4 feet above the ground while those completed after April 28 averaged 8.5 feet. This difference is significant ("t" = 6.63), and the increased height of late nests thus obtains within all species as well as between species.

Nesting Materials

The heronry must not only provide these herons with a potential territory, but must also provide them with nest building materials which are gathered outside the territory. These herons all make their nests out of small sticks and twigs, collected in or adjacent to the heronry. Snowy Egrets pick twigs up off the ground. Louisiana Herons usually do likewise, but sometimes break twigs off dead branches and limbs near or on the ground. Cattle Egrets and Little Blue Herons break living and

dead twigs off trees and bushes. Cattle Egrets tend to limit their twig gathering to the upper and outer reaches of the trees, where they take smaller twigs. Late in the 1959 nesting season, Cattle Egrets took nest material from trees around the edge of Lake Alice; this was the first year that any of the herons gathered nesting material away from the heronry. In 1960, Cattle Egrets again took twigs from the lakeshore, but started doing so in the middle of the nesting season, much earlier than in 1959. By the end of the 1960 season they were bringing twigs back from more than half a mile away. These differences in the sources of building twigs tended to reduce, though by no means eliminate, competition among species for this material. That these differences may not be characteristic of the species everywhere is suggested by Meanley's (1955) observation that in Arkansas, Little Blue Herons gathered nesting material from the water beneath the heronry that he studied.

The herons do not feed in the heronry and there appears to be little in this area besides nest sites and nest material which might be in short supply and over which interspecific competition might arise. Other benefits the birds derive from the heronry, including association with one another, probable freedom from predation, and other benefits, are much more subtle, and do not readily lend themselves to quantitative description.

The Island Location

One feature the Lake Alice heronry has in common with most other Florida heronries, is its location on an island. Florida heronries not located on islands are usually found in trees growing in rather deep

water. Furthermore, fresh water heronries in Florida tend to be located where there are alligators. Two salt water heronries near Cedar Key, Florida, are on islands which also support large populations of cottonmouths (Agkistrodon piscivorus, Wharton, 1958). This almost universal "island" location of heronries may help free them from mammalian predators. Raccoons (Procyon lotor) were specifically implicated in the destruction and abandonment of a Roseate Spoonbill (Ajaia ajaia) colony in Florida Bay (Allen, 1942). The absence of raccoons and other mammals from Florida heronries suggests that the heronries are not accessible to them, and is probably a critical factor in the permanence of the nesting areas. Other requirements, such as nest sites and nesting materials, are certainly more widely available to herons than is freedom from mammalian predation.

Feeding Niches

The four herons occupy different feeding niches. That of the Cattle Egret is clearly unique. Feeding habits of the other three species superficially appear essentially identical, but more detailed observations of adult feeding behavior, and analysis of pellets regurgitated by young birds reveal that these four species diverge in feeding preference and behavior.

The Cattle Egret feeds exclusively on terrestrial food, usually in association with cattle or other grazing animals, although sometimes it forages alone. It captures insects, primarily grasshoppers and crickets, and upland frogs.

The three other herons feed mostly on aquatic prey. The Snowy Egret usually forages in shallow water where it captures small fish--primarily

mosquitofish--and a few tadpoles and insects. The Little Blue Heron feeds in slightly deeper water and takes mostly amphibians, large ranid tadpoles and frogs, and a large volume of fish, primarily topminnows. The Little Blue Heron takes larger fish than any of the other herons. The Louisiana Heron feeds in deeper water than even the Little Blue Heron, taking medium to small-sized fish, primarily flagfish. It is the most confirmedly piscivorous heron studied.

Apparently feeding areas must be sufficiently close to the breeding place that the birds can make several round trips between the two places during the rearing periods. They must provide an adequate concentration of suitable prey for the birds. However, the feeding ecology of the heronry has not been adequately studied.

Establishment and Abandonment of Heronries

To be selected as a breeding place by herons, a site must, besides being reasonably close to feeding areas, also offer suitable space for territories and supports for nests, must have an adequate supply of nesting materials, and must be free from excessive predation, which apparently means complete or nearly complete absence of mammalian predators. Places offering appropriate territorial and nest sites and nesting material, near suitable feeding areas appear to be plentiful, but the number of such places that are also free of predatory mammals is probably smaller. Floating islands, small mangrove islets, islands with large cottonmouth populations, and spoil banks in lakes and bays, have already been mentioned as areas supporting heronries. In recent years heronries have been established in cypress trees in Florida phosphate settling ponds. These areas have one feature in common,

besides their aquatic location: they do not support raccoon populations, and are difficult if not impossible of access to raccoons.

In some cases, heronries have been abandoned simply because of human disturbance. As an extreme example, all the nest trees of a small heronry near Brooksville, Florida, were removed during 1960, and there remains only a treeless, bushless pond. But herons sometimes leave nesting areas for no apparent reason, as they abandoned Bivin's Arm near Gainesville in 1948. Except for those caused by human interference, no cases of heronry abandonment have been satisfactorily explained.

The herons may be an important factor in altering their own breeding habitat and making it unfit. Even a medium-sized colony of birds such as that breeding at Lake Alice is quite hard on the nesting vegetation. The bushes and trees that best satisfy the herons' requirements are typically those growing in marginal situations. The weight of roosting birds breaks off limbs. Twig hunting males seriously prune the trees and apparently break off every twig available in the heronry. Cattle Egrets had to leave the heronry to hunt twigs during the latter part of 1959 and 1960. The total impact of the birds of their nesting substrate is great, and when the extent of the suitable habitat is small as it is at Lake Alice, the birds can probably effectively destroy the habitat. In a large area such as Bird Island, in Orange Lake, the effect would be relatively less than at Lake Alice and the birds would probably not be able to do much permanent damage.

Herons often establish breeding areas in vegetation killed by artificial flooding, as at Lake Alice. Such areas can be expected to provide suitable nesting places for only a few years, unless the dead

trees are supplemented by the growth of new aquatic trees and bushes. At Lake Alice new growth has been inadequate, and each year since 1957 there has been less nesting substrate. Since 1959 the White Ibis have failed to nest at Lake Alice, and the vegetation has continued to decline, and if the present trend continues the place will probably be deserted by the herons within a few years.

Thus, there are several factors other than human interference that may cause herons to abandon an established breeding area. For example, the failure for any reason of the heronry trees and bushes to grow and replace themselves would decrease the number of territorial and nest sites, and the amount of available nesting material. However, as was said above, Cattle Egrets at Lake Alice gather some of their nesting material away from the heronry. The heronry might become accessible to mammalian predators, as a result of lowered water levels or in any of several other ways. Although there is, as yet, no evidence for it, the heron ectoparasite population conceivably might, over a period of years, increase to a density that would cause the birds to leave. The available feeding areas might be so altered, for example by changed water levels, as to be no longer suitable. The final explanation of why herons abandon a long used breeding place will probably involve at least one such subtle or gradual change.

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This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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